Wetlands

Plant community compositional stability over 40 years in a Fraser River Estuary tidal freshwater marsh

--Manuscript Draft--

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Abstract:	Long-term data sets documenting temporal changes in vegetation communities are uncommon, yet imperative for understanding trends and triggering potential conservation management interventions. For example, decreasing species diversity and increasing non-native species abundance may be indicative of decreasing community stability. We explored long-term plant community change over a 40-year period through the contribution of data collected in 2019 to two historical datasets collected in 1979 and 1999 to evaluate decadal changes in plant community biodiversity in a tidal freshwater marsh in the Fraser River Estuary in British Columbia, Canada. We found that plant assemblages were characterized by similar indicator species, but most other indicator species changed, and that overall α-diversity decreased while β-diversity increased. Further, we found evidence for plant assemblage homogenization through the increased abundance of invasive species such as yellow flag iris (Iris pseudacorus), and reed canary grass (Phalaris arundinacea). These observations may inform concepts of habitat stability in the absence of direct anthropogenic disturbance, and corroborate globally observed trends of native species loss and non-native species encroachment. Our results indicate that within the Fraser River Estuary, active threat management may be necessary in areas

	of conservation concern in order to prevent further native species biodiversity loss.
Response to Reviewers:	Revisions were made according to Reviewer 2 & 3 comments; we thank these reviewers for their insightful and constructive critiques. We have explained these revisions by each section of the manuscript, and indicated which reviewer we addressed for each revision. Introduction Reviewer 2, Line 57 (revised ms line 55): revised to include daily & monthly changes due to tide cycles, and distinguished these from processes which occur on longer timescales, such as sediment accretion or marsh subsidence. Reviewer 2, Line 71 (revised ms line 70): changed wording from "…these habitats to resist change or recover from disturbance" to "…these habitats to adapt to disturbance." Reviewer 3, Line 92 & Reviewer 2, Line 93: Both reviewers had concerns the hypothesis as originally phrased required substantial supporting data to link abiotic changes (e.g., altered river hydrology, sedimentation, etc.) to answer the question. We agree that these processes are important for understanding floristic responses, however it wasn't the original intent of the study nor presently possible to include these data. We revised the question (see revised ms lines 91-93) to ask "How have the tidal freshwater marsh assemblages in Ladner Marsh changed over the past 40 years? We would expect substantial changes in composition and abundance of species dominating assemblages to offer clues of processes driving change." We also advise in the Discussion on potential ways to include abiotic data in future studies to understand mechanisms driving floristic change. Methods To address Reviewer 2's consideration of reed canary grass as a native species, we include a brief acknowledgement of the native/non-native taxonomic debate of reed canary grass in Methods subsection Vegetation identification. We include reference to local regulatory classification, and pollen analysis to support our position treating this species as non-native in wetland communities around the Salish Sea. See revised ms lines 179-186 Reviewer 2, Fig. 1: added a scale bar & north arrow to all maps Reviewer 2, Fig. 2D: delineation of dominant vegetation patches was confused with elevational zonation; we clarified this distinction in the figure caption. Reviewers 2 & 3 suggested some kind of explanation of elevation and relationship to vegetation zonation along elevation gradients. In Methods subsection 'Site history & context' we clarified that the elevation gradients observed along these transects are not so great as to affect species zonation. See revised ms lines 108-119. Reviewers 2 & 3 wanted elaboration on how/why certain transects or plots were omitted, as we described environmental changes such as channel migration and shrub encroachment as the main reasons for omitting plots. We addressed this by clarifying how Transect Q was impacted by riparian thicket encroachment, likely from immediately adjacent municipal infrastructure (revised ms lines 189-195). We also provided more detail about how inaccuracy of transect relocation may have resulted in differences in overall transect length (with speculation on some minor bank erosion also contributing to different transect length) (revised ms lines 201-210). We also provided clarification for how plot placement in 2019 would have resulted in different numbers of plots per transect, and describe how the most spatially comparable plots between all three sampling years were selected in order to make fair comparisons at the plot and transect scales (revised ms lines 201-210). This should help resolve some of the concern for not explaining broad abiotic changes: our original phrasing in the first ms submitted may have caused reviewers to infer that abiotic changes were more significant than we believe them to be. While we address these concerns (as noted elsewhere), we do not feel that abiotic changes in the marsh were the primary or secondary causes for differences in plot and transect placement over time.

	Reviewer 3 specifically requested elaboration on exact methodologies to assess plant cover. We added substantial text in four new subsections to clarify the sampling design & harmonization between observations, plot-scale sampling details, and clarify differences between the datasets. (revised Methods, subsections ‘Sampling design & harmonization between observations,’ ‘Plot-scale sampling,’ ‘Vegetation identification,’ and ‘Differences between datasets.’) In the section on analytical approach, we clarified that we elected to identify three main clusters (forgoing a common distance level break point, as suggested by Reviewer 3) to facilitate comparison of species composition & abundance between three assemblages common to all datasets (revised ms line 219-220). Because each of the three clusters identified in each dataset had consistently common indicator species (Sedge, Bogbean, Fescue), we suggest maintaining these three groupings between datasets affords the most intuitive way to discuss how composition & abundance is shifting within the marsh, especially with reference to observations made in Bradfield & Porter (1982). We also address this in the Results, as explained next. Results We acknowledge that analysis of the clusters at a common distance level (e.g., Euclidean distance = 35 as per Reviewer 3) would result in changing the number of groups compared, and this approach would also support our conclusion that the plant community is becoming homogenized throughout this marsh. However, indicator analysis under this approach removes Carex lyngbyei, a key marsh species, as an assemblage/indicator species only in 2019, and combines the Bogbean & Fescue groups in 1999 (but not in the 1979 or 2019 data). We feel the cumbersome explanation of these shifts in the groupings would detract from the overall interpretation of homogenization, and would not provide any further clarity on potential mechanisms for the changes. We also acknowledge that exploration of finer groupings at a lower distance level (as per Reviewer 3; e.g., Euclidean distance = 10) would allow for more discussion on finer shifts in plant composition and abundance, however, thoroughly explaining these shifts would similarly detract from the main message of homogenization without contributing benefit of identifying mechanisms. Pursuant to this, Reviewer 3 questioned whether the ‘Fescue’ group should be renamed, as the namesake indicator species (Fescue, Schedonorus arundinaceus) shifts in its level of importance in the indicator species analysis. We propose that it is useful to have a common species to identify with each assemblage for sake of clear communication, and Schedonorus arundinaceus is the only common species for each observation period. Additionally, if we were alter the assemblage name for the Fescue group to reflect its shifting importance in the indicator species analysis, we would also need to do this for the Bogbean group, which further contributes to the challenge of renaming the assemblages and potentially leading to awkward communication of results. To alert readers to this convention, we include a brief statement in the Results in the explanation of indicator species analysis (revised ms line 279-282). We also amended Table 1 (indicator species results, revised ms line 328) to include the Indicator Value index as suggested by Reviewer 3, however, this creates a very wide table that requires landscape page orientation – we defer layout formatting to the editorial staff, and are happy to revise table dimensions to fit journal requirements. We agree that an explanation of spatial relationships of the changes observed would be valuable to identify which areas of the marsh may be changing (per Reviewer 3). To this end, we included a bar chart figure of percentage of plots per transect in each cluster assemblage (Fig. S3). In the Results we explain how proportion of plots belonging to the same assemblage cluster appear quite stable along some transects (e.g., transects W and X). This allows us to speculate that some spatial trends in assemblage occurrence may be due to differences in transect placement between observation time points (e.g., transects U and V), or may be due to plant community turnover. (Revised ms lines 295-301, additional supplemental figure Fig. S2). We agree with Reviewer 3 that the frequency with which we refer to Table S5 indicates the table is important to the Results. However, because the table is four pages long we defer to the journal’s decision about whether to format it for inclusion in the Results section or as a supplemental.

	Discussion Reviewer 2 indicated hydrogeomorphological processes would need to be discussed to support the elimination of some plots from the survey due to inaccessibility and potential altered channel morphology, and Reviewer 3 wanted to see robust discussion of changes to the physical environment over time. While altered hydrogeomorphological changes are suspected drivers of change across the marsh, we feel it is beyond the scope of this study to pursue an analysis of hydrologic changes and sufficiently link these to observed plant community changes. Similarly, data on sediment transport rates in this river system would be incomplete for making a strong case directly linked to observed changes. For example, we could obtain data from sediment dredging operations, but this would not address total sediment loads. We could attempt to calculate sediment loss due to increased impervious cover on the landscape, but this would be a proxy (at best) for understanding altered sediment loading into the estuary. Instead, we have emphasized that the majority of plots eliminated from Transect Q (as reported in the original 1982 publication by Bradfield & Porter) were due to overgrowth of Himalayan blackberry, rather than channel migration. Other plots that were omitted from this analysis were clarified as likely being due to transect relocation challenges between timepoints. We acknowledge the potential for some of this relocation challenge could be due to some bank erosion, but emphasize that this would be minor (as assessed by inspection of aerial photography), and emphasize the discrepancies in transect placement as due to different observers without permanent reference markers; please also refer to revised Methods comments. Reviewer 2, Line 339 (revised ms line 413): we indicated loss of root biomass would alter sedimentation rates; Reviewer 2 questioned whether it was only the roots or also above-ground biomass that traps sediment. We amended the language to indicate sediment trapping may be affected by altered vegetation structural complexity to indicate inclusion of any above and below-ground structures that serve to trap sediment. Reviewer 2, Line 353: we indicated biodiversity loss can have trophic consequences, and included a reference to 'top-down trophic interactions.' Reviewer 2 pointed out this phrase was included without further explanation, so we elected to remove it as any further elaboration becomes tangential to our intended scope. Reviewer 2, Line 361 (revised ms line 434): we focused on altered sedimentation rates as a potential mechanistic driver of change; Reviewer 2 suggested relative sea level rise as a factor, which has been added to the statement of potential mechanisms that could result in areas with greater saturation. Reviewer 2, Line 366 (revised ms lines 439-440): 'scouring tidal surge' wasn't a clear way to exemplify natural disturbance. We elected to remove reference to 'natural disturbance,' as the examples we could identify are confounded by anthropogenic influence over the course of our observations. For example, a 'scouring tidal surge' would be an extreme storm event with sufficient power to thrust large logs across the marsh, ripping out vegetation. However, current abundance of such logs within the estuary are mostly due to logging industry (rather than due to natural senescence and introduction to the estuary system). Our main point here was to indicate press stressors from anthropogenic sources are likely having an effect, despite not seeing dramatic changes commonly associated with human impacts (e.g., industrial development, agriculture, etc.); inclusion of natural disturbance in this sentence is tangential.

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13th February, 2023

Dr. Marinus L. Otte
Editor-in-Chief
Wetlands

Dear Dr. Otte,

We are submitting an original research article to *Wetlands* entitled "Plant community compositional stability over 40 years in a Fraser River Estuary tidal freshwater marsh" for publication consideration. We have used two historical datasets and one new dataset to address the question 'how has plant community composition and abundance changed over 40 years in a protected conservation area?' We have found evidence for declines in native species richness, and increases in homogenization of compositional abundance, despite conservation status of this habitat and absence of direct anthropogenic disturbance (e.g., industrial or recreational development).

We feel this work is useful to inform conservationists and land managers of changes to a conservation habitat used as an ecological conservation and restoration benchmark. We feel it is particularly timely as the region grapples with how to appropriately respond to threats of sea level rise, which would submerge this conservation area within 50-100 years. Moreover, we feel this study is of broad international interest as it provides a case example of biodiversity loss in an ecosystem which is typically underrepresented in longer-term monitoring studies (as compared to inland wetlands, and other ecosystems such as grasslands or forests). If this manuscript is selected for peer review, we suggest the following reviewers (listed alphabetically by last name) with relevant expertise to evaluate this work:

- Dr. Thorsten Balke, University of Glasgow, Thorsten.Balke@glasgow.ac.uk; biophysical interactions in salt marshes.
- Dr. Amy Borde, Pacific Northwest National Laboratory, amy.borde@pnnl.gov, tidal wetland restoration & monitoring, including invasive species control.
- Dr. Tjeerd Bouma, Royal Netherlands Institute for Sea Research, tjeerd.bouma@nioz.nl ; vegetation as bioengineers in coastal ecosystems.
- Dr. Sally Hacker, Oregon State University, sally.hacker@oregonstate.edu; community structure and function of coastal ecosystems, including invasive vegetation ecology.
- Dr. Tracy Quirk, Louisiana State University, tquirk@lsu.edu; plant community ecology & human impacts on wetland ecosystems.

To the best of our knowledge, none of these suggested reviewers have any conflict of interest including financial or personal connection to our work.

Thank you sincerely for your consideration of our manuscript,

Stefanie L. Lane

Title Page

Plant community compositional stability over 40 years in a Fraser River Estuary tidal freshwater marsh

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Abstract

Long-term data sets documenting temporal changes in vegetation communities are uncommon, yet imperative for understanding trends and triggering potential conservation management interventions. For example, decreasing species diversity and increasing non-native species abundance may be indicative of decreasing community stability. We explored long-term plant community change over a 40-year period through the contribution of data collected in 2019 to two historical datasets collected in 1979 and 1999 to evaluate decadal changes in plant community biodiversity in a tidal freshwater marsh in the Fraser River Estuary in British Columbia, Canada. We found that plant assemblages were characterized by similar indicator species, but most other indicator species changed, and that overall α-diversity decreased while β-diversity increased. Further, we found evidence for plant assemblage homogenization through the increased abundance of invasive species such as yellow flag iris (*Iris pseudacorus*), and reed canary grass (*Phalaris arundinacea*). These observations may inform concepts of habitat stability in the absence of direct anthropogenic disturbance, and corroborate globally observed trends of native species loss and non-native species encroachment. Our results indicate that within the Fraser River Estuary, active threat management may be necessary in areas of conservation concern in order to prevent further native species biodiversity loss.

Keywords

shifting baselines; reference conditions; dispersal networks; species turnover; conservation land management

Acknowledgements

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Introduction

In a time of rapid global change, temporal shifts in plant community composition can indicate ecosystem stress response and inform conservation management interventions. Shifts in community-dominant species may be indicative of interspecific interactions such as facilitation (Bruno, 2000), succession (Butzeck et al., 2016), or cycles of population dynamics (Holling, 1973). Alternatively, changes in community-dominant species paired with loss of native species diversity and increasing abundance of non-native species may indicate loss of stability through loss of functional redundancy (Donohue et al., 2016; Tilman, 1999; Palmer et al., 1997). In turn, this may indicate reduced resistance to change or capacity to recover from disturbance, known as resilience (Tilman et al., 2006; Bai et al., 2004). Furthermore, the local loss of native species may have stronger negative impacts on regional biodiversity persistence when the regional pool of potential species is reduced or environmentally constrained (Lepš, 2004; Hanski, 1982). Characterization of plant community changes on decadal timescales contributes to observation of meaningful long-term patterns of compositional stability, and is instructive for developing hypotheses to test drivers of disturbance, especially in data-deficient, dynamic landscapes heavily impacted by anthropogenic activities such as estuaries (Underwood et al., 2000; Ovaskainen et al., 2019).

Estuaries are at the terrestrial-marine interface where hydrogeomorphic and ecological changes occur according to daily and monthly tidal cycles, as well changes due to ecosystem scale processes such as sedimentation or marsh subsidence on annual, decadal, and millennial timescales (Pasternack, 2009). Estuarine habitats support high species richness, including species at risk (Kehoe et al., 2021), and are important carbon reservoirs (Gailis et al., 2021; Douglas et al., 2022). Because these ecosystems will experience accelerated change under sea level rise, they are of increasing conservation concern (Brophy et al., 2019); understanding estuarine habitat changes and implications for habitat stability can inform global change resilience strategies. Estuaries in North America are of particular conservation importance in the Pacific Northwest (PNW) because their pathways of retreat or expansion are often spatially restricted by fjord topography (Emmett et al., 2000), whereas estuaries along the Atlantic coast may spread along expansive coastal plains. Tidal freshwater marshes occur at the upper reaches of estuaries and in the PNW they are particularly important as early transitional habitat along a salinity gradient for anadromous salmonids (Davis et al., 2021; Chalifour et al., 2019). The Fraser River Estuary is the largest estuary in British Columbia and of irreplaceable ecological and commercial value, yet has lost 85% of floodplain and 64% of stream habitat in the Lower Fraser watershed (Finn et al., 2021), emphasizing the need to understand the condition of remaining estuarine habitat. Estuary conservation efforts are intended to protect coastal municipalities and provide sufficient habitat for wildlife. Stability of plant communities within tidal marshes contributes to the ability of these habitats to adapt to disturbance (Holling, 1973). A barrier to understanding community stability, including within estuaries, is the lack of long-term data. In the absence of long-term monitoring, historical datasets can provide a 'snapshot' of species compositional variation over time. One such opportunity exists in the Fraser River estuary, British Columbia, Canada in an area called Ladner Marsh (Fig. 1). Despite large-scale industrialization and urbanization within the region, Ladner Marsh has escaped direct industrial development, and to the best of our knowledge has not experienced major anthropogenic disturbance such as diking or agriculture in the past 50 years.

Two historical studies conducted in Ladner Marsh (Bradfield & Porter, 1982; Denoth & Myers, 2007) used similar methods to document floristic diversity. Bradfield & Porter (1982) tested whether species dominating the community statistically characterized distinct sub-community assemblages within the marsh. Their analysis distinguished three assemblages, each dominated by a unique species: Sedge (*Carex lyngbyei* Hornem.), Fescue (*Schedonorus arundinaceus* (Schreb., formerly *Festuca arundinacea*) Dumort., nom. cons.), and Bogbean (*Menyanthes trifoliata* L.). They postulated that edaphic factors drove assemblage distribution: that the Bogbean assemblage occurred on waterlogged soils, the Fescue assemblage on well-drained soils mostly along levees, and the Sedge assemblage along channel edges with greater inundation frequency. Twenty years later, Denoth

& Myers (2007) repeated the sampling methods to test relationships between non-native purple loosestrife (*Lythrum salicaria* L.) and native Henderson's checker-mallow (*Sidalcea hendersonii* S. Watson), a threatened species. While these studies independently characterize different community metrics, these datasets provide the opportunity to repeat observations and characterize long-term plant community changes to inform inferences about habitat stability. We used three observational datasets spanning four decades to answer the following questions:

(1) How have assemblages in Ladner Marsh changed over the past 40 years? We would expect substantial changes in composition and abundance of species dominating assemblages to offer clues of processes driving change.
(2) Are assemblages characterized by similar indicator plant species? If not, what species changes are associated with each assemblage? We expect that increasing abundance of non-native species over time would result in a greater net loss of native species.
(3) Is the mean species diversity (α-diversity) and variation (β-diversity) within and between assemblages constant between the three sampling periods (1979, 1999, 2019)? If the plant community is stable, we expect little change in α-diversity and β-diversity.

Methods

Site history & context

The Fraser River is the largest watershed catchment in British Columbia, covering one quarter of the province (Finn et al., 2021). The current extent of the Fraser River Estuary spans 2,814 ha, one-third of which lies within the South Arm Marshes Wildlife Management Area, which was formally protected in 1991 (Schaefer, 2004) (Fig. 1B). Ladner Marsh occupies approximately 100 ha within the South Arm Marshes, bounded to the east by urban and industrial development and to the west by the Fraser River (Fig. 1).

Plant species common to these habitats are generally herbaceous, and the community is largely dominated by sedges, grasses, and rushes, with a diversity of herbaceous flowering species (hereafter, forbs). Patterns of species distributions within tidal marshes are driven by elevation gradients, which filter species according to inundation and salinity regimes (Bertness & Ellison, 1987). The areas surveyed in Ladner Marsh (with the exception of Transect Q, omitted as explained in section 'Differences between datasets') correspond to elevations between the mean high water (MHW, approx. 1.1 m above mean sea level) and mean higher high water (MHHW, approx. 1.4 m above mean sea level) (as measured in Lane, 2022). Many species encountered in the surveys conducted are not restricted to these elevation ranges; emergent vegetation begins at the local mean tide extending to the upper limit of tidal inundation (Janousek et al., 2019). Thus, the elevation range of surveyed areas that we compare here occurred within a sufficiently restricted tidal elevation range that we do not expect elevation gradients and related hydrologic/salinity regimes to be a strong driver of species distributions within the areas surveyed.

Sampling design & harmonization between observations

Our main goal was to sample the vegetation in a representative way to allow comparison with the datasets collected in 1979 (Bradfield & Porter, 1982) and 1999 (Denoth & Myers, 2007). This publication will reference dates the data were collected, rather than publication dates of the corresponding studies.

In the original 1979 study, eight transects (Q-X) were laid out in a subjective fashion to cross through the main features of vegetation diversity at Ladner Marsh (Fig. 1 in Bradfield & Porter, 1982). All transects spanned a similar elevation range across the marsh platform, with the three main plant assemblages (Sedge, Fescue, Bogbean) separated by apparent changes in hydrological conditions along transects.

In the 1999 study, Bradfield & Porter's (1982) Fig.1 was used to visually approximate the locations of transects to repeat the vegetation survey (Denoth & Myers, 2007). In this study (2019 survey), transect locations were determined by overlaying Bradfield & Porter's (1982) Fig. 1 on a georeferenced basemap, aligning prominent features such as tidal channel tributary junctions, marking GPS locations in Avenza Maps (Avenza Systems Inc., Ontario, Canada, v. 3.2), and finding these points in the field (Fig.1C). Difficulties arising from the inexact relocations of transects in the 1999 and 2019 surveys, and aggressive shrub encroachment along transect Q, resulted in an incomplete resampling of all eight transects from the original 1979 survey (further explained below). To evaluate the potential for differences in transect relocation to affect trends observed in the data, or to evaluate marsh-wide spatial trends in plant composition, we calculated the percentage of plots clustered in each assemblage group for each transect.

All three studies used a semi-systematic approach for determining locations of 1x1 m quadrats along transects. In the 1979 study, quadrats were mainly located at 10 m intervals along transects although this varied in places from 2-20 m depending on local changes in the vegetation (Bradfield & Porter, 1982). In the 1999 study, an attempt was made to follow the quadrat spacing shown in Bradfield & Porter's (1982) Fig. 3 regardless of perceived vegetation changes along transects. For the 2019 study, quadrat placement was guided by visual assessment of vegetation patchiness along transects. If patches dominated (>50 % cover) by one or two species (not necessarily the three assemblage identifiers) continued more than 10 m of transect length, or if no dominant species was evident, we sampled every 10 m of transect length (Fig. 2D). No patches were so small that the 1 m^2 plot was less than 1 m from the boundary of the next patch. Such fine-scale variations in decisions for quadrat placement among the three studies were considered inconsequential for the broader scale assessments of assemblage changes over time.

Plot-scale sampling

Species were recorded if their most basal stem originated within the 1 m^2 quadrat, and cover within the plot was considered for all above-ground vegetation that occurred within the quadrat boundary; vegetation overhanging the quadrat from individuals whose basal stems originated outside the quadrat boundary was not considered. In the instance where the basal stem was inside the plot, but aerial vegetation extended beyond the boundary of the quadrat, we only considered vegetation cover for portions of the plant within the boundary of the quadrat. We treated each ramet of rhizomatous species such as *Carex lyngbyei* or *Juncus* sp. as individuals, rather than attempting to delineate extent of each continuous rhizome of the genetically distinct individual. For these species, whenever the quadrat fell on top of an individual ramet, the ramet was considered in the plot if more than 50% of the leaves emerging from the ramet were immediately under or inside the quadrat boundary. Aerial plot cover was estimated by modified Braun-Blanquet cover classes used by Bradfield & Porter (1982) and Denoth & Myers (2007), where cover class 0 = 0% cover (absent), cover class 1 represents < 25% cover, cover class 2 represents 25-50% cover, cover class 3 represents 50-75% cover, and cover class 4 represents > 75% cover. Owing to consultation with one of the co-authors (Gary Bradfield) in the 1999 and 2019 studies, differences in between-observer cover estimation were considered minimal.

Vegetation identification

For all sampling years, observation of vascular plant species was conducted in early summer when species are identifiable by sexual reproductive traits, but before senescence (approx. June – July). In all datasets, most plants were identified to species according to Hitchcock & Cronquist (1973), although a few were identified at higher taxonomic levels due to insufficient identifying characteristics (n = 6 to genus, n = 2 to Family; see Table S7). To account for changes in nomenclature revision over time, all datasets were harmonized to use the most recently accepted species name as reported in the PLANTS Database of the United States Department of Agriculture, Natural Resources Conservation Science [USDA NRCS]. For example, in the instance of *Agrostis* species, we assumed *Agrostis alba* L. identified in 1979 and 1999 was synonymous with *Agrostis stolonifera* L. in

2019. All species and their synonymous nomenclature from prior data collection years are available in Supplemental Table S7.

We elected to classify *Phalaris arundinacea* as non-native to align our treatment of the species with the designation provided by the British Columbia Ministry of Environment Species & Ecosystems Explorer (B.C. Conservation Data Center, 2023), which is the authoritative source for species conservation information for the province. While molecular analysis has confirmed *P. arundinacea* was native to North America prior to European colonization (Anderson et al., 2021), regional pollen studies have demonstrated some evidence for its absence in wetlands around the Salish Sea (Townsend & Hebda, 2013). Perhaps most important to consider is that hybridization of native with introduced varieties have resulted in aggressive invasive attributes, resulting in this species being of high management concern in Salish Sea Ecosystems (Sinks et al., 2021).

Differences between datasets

In 1999 and 2019, some plots were omitted due to access or relocation issues (Table S1). Most notably, transect "Q" (n = 7 plots) was omitted in 1999 and 2019 due to inaccessibility. In 1979, this transect was placed within approx. 100 m of Ferry Rd, which forms the eastern boundary of the marsh by an approx. 2 m elevated grade to keep the road above high tide elevations. In this portion of the marsh, riparian forest with an understory of non-native Himalayan blackberry (*Rubus armeniacus* Focke) grew so densely that by 2019, access to the transect would have required significant and costly vegetation removal. The encroachment of blackberry and riparian thicket were also a challenge preventing surveyors in 1999 from accessing this area. Thus, data from transect Q are not included in the present analyses.

The 1999 survey approximately located all plots from transects R-X from the original 1979 survey; however, the number of plots along these transects differed in 2019. This is partially due to the surveyors in 1999 seeking to exactly relocate original plot locations, while in 2019 our objective was to place the plots according to visual perceptions of shifts in dominant species. Besides the plots omitted by not sampling transect Q, we noted a total of 20 fewer plots surveyed in 2019 (Table S1). This is most likely due to our methods in 2019 placing plots to characterize patches dominated by distinct species, resulting in number of plots being contingent on vegetation composition rather than spatial accuracy. Additionally, we acknowledge that spatial inaccuracy of transect relocation would result in different total transect lengths, and thus a different number of plots to be sampled along the transect. We also speculate there may have been some bank erosion resulting in wider channel mouths where some transects originated or ended, resulting in shorter transects overall. Visual comparison of satellite imagery suggests that erosion would have been minor, but not absent. To reconcile these differences, we excluded 1-4 plots per transect from the 1979 and 1999 datasets that had the least potential for spatial proximity to plots sampled in 2019 in order to compare an equal number of plots between sampling years along a similar length of transect (Table S1).

Analyses

All analyses were performed in R v. 4.2.1 (R Core Team, 2022). We performed cluster analysis on species composition and abundance at the plot scale for each dataset. Similar to Bradfield & Porter (1982), we used Euclidean distance as the measure of plot dissimilarity ("stats," R Core Team). Following Legendre & Legendre (2012), we also performed cluster analysis using Bray-Curtis dissimilarity to compare with Euclidean distance and found no meaningful difference in results from the two distance measures (Fig. S1).

For each dataset we identified three assemblages, defined by the 3-group cut-level for each dendrogram, to facilitate direct comparisons of changes in vegetation properties over time. Species indicator analysis was used to determine which species abundance characterized each assemblage ("indicspecies,"R package De Cáceres & Jansen, 2016). Indicator Value (IndVal) association indices between species and clustered assemblages were calculated using an abundance-based point biserial correlation coefficient (multipatt func =

"r.g"), and significance of associations was tested by permutational analysis (Dufrêne & Legendre, 1997). We also performed indicator analysis on the Bray-Curtis clusters to confirm that significant indicator species were comparable between the two distance measures (Table S2). All species' mean cover abundance is summarized in Table S6.

Community diversity calculations for each year of observation followed Whittaker (1975), with α-diversity calculated as the mean number of species per plot within an observation year and assemblage, and β-diversity calculated as the total number of species within the assemblage divided by α-diversity. These calculations were also performed on all data recorded for each observation year to generate community-wide measures of diversity. To address inconsistent numbers of plots grouped into assemblages each year, diversity metrics were bootstrapped 10 times using the minimum number of plots observed in an assemblage each year (n = 18) (Table S3).

Community turnover for each assemblage was measured using the "codyn" R package (Hallett et al., 2016). Total species turnover (total magnitude of change), species gained (appearances), and species lost (disappearances) were calculated as a percent change for each assemblage between 1979–1999, and 1999–2019. Total turnover was calculated as a ratio of the absolute value of species gained and lost to the total number of species observed in both timepoints.

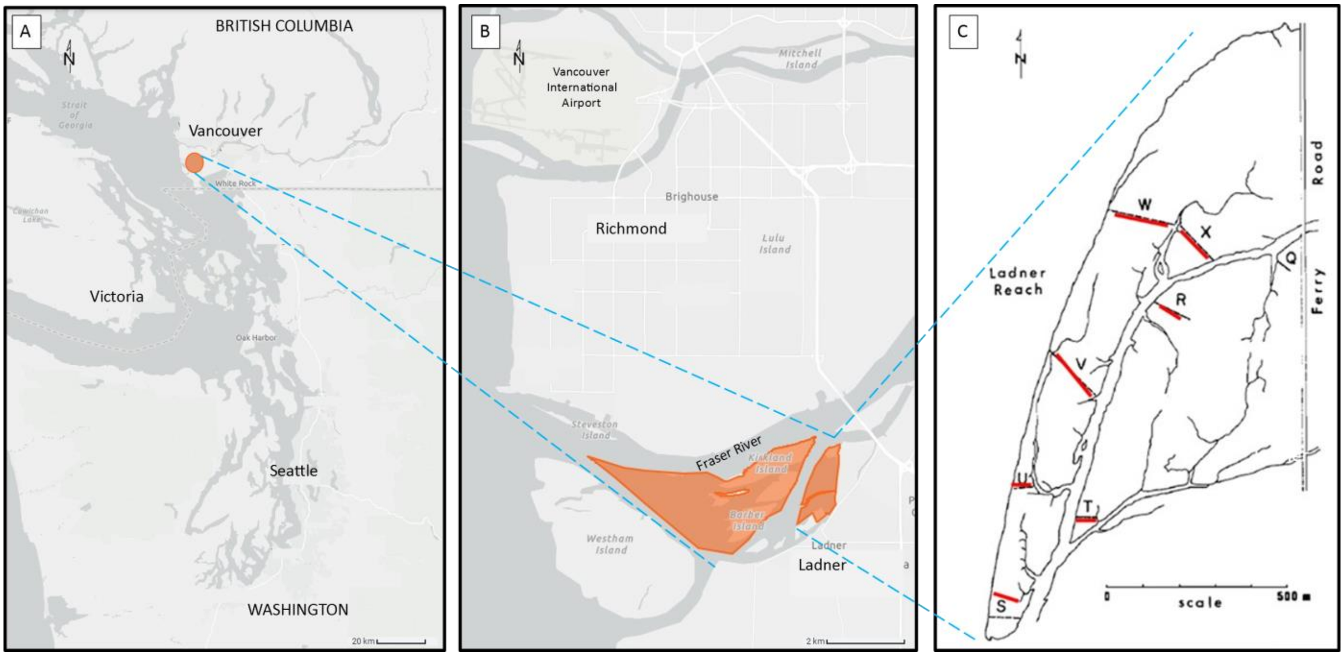

Fig. 1 Study area location and sampling design. (A) Regional location of the Fraser River Estuary in southwestern British Columbia, Canada, (B) South Arm Marshes Wildlife Management Area (highlighted in orange), (C) Ladner Marsh with overlay of 2019 transect locations (shown in red) on original transect map from Bradfield and Porter (1982). Base maps (A, B) generated by iMap published by the B. C. Conservation Data Center (Victoria, BC, Canada, https://maps.gov.bc.ca/ess/hm/imap4m).

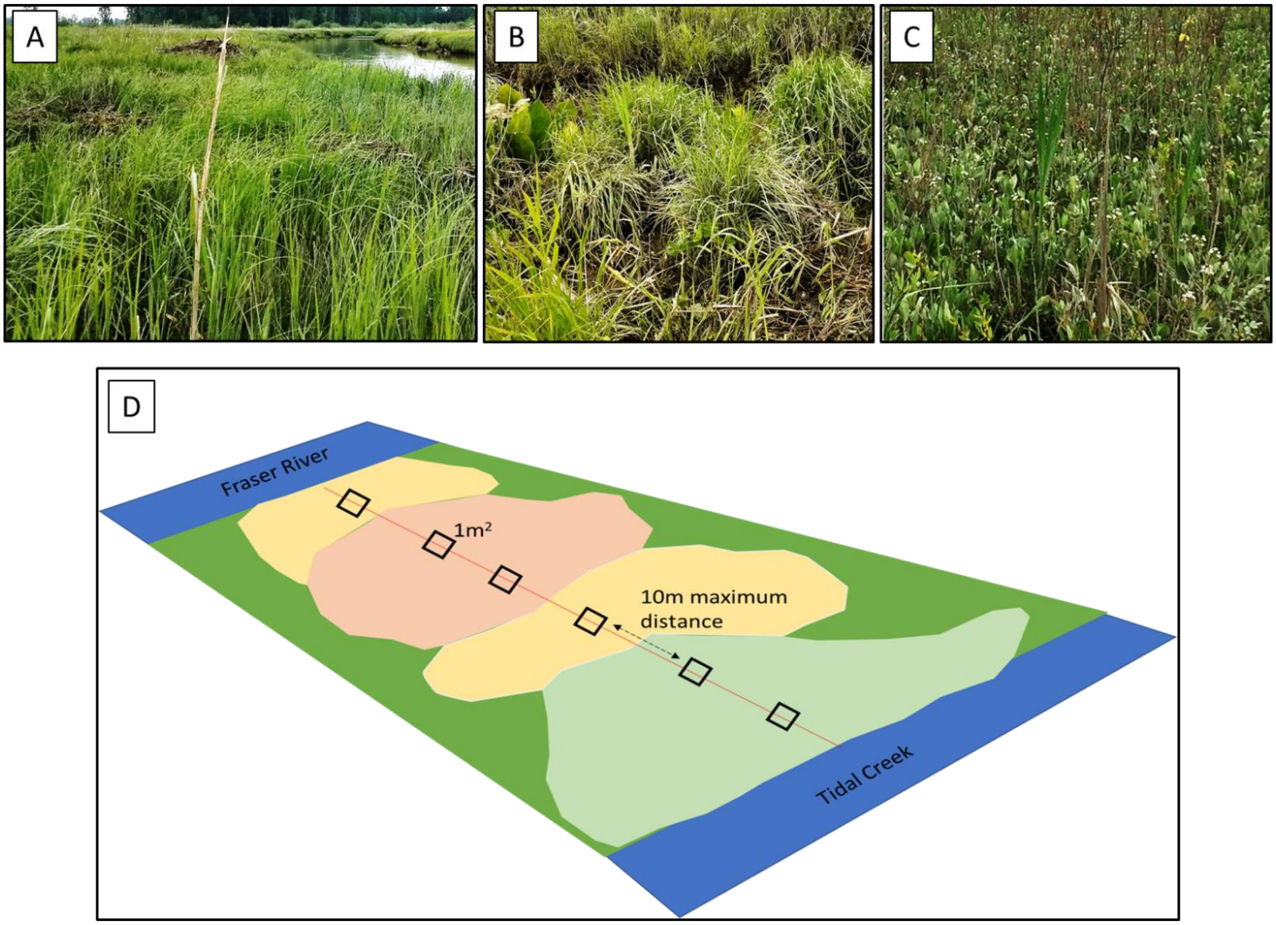

Fig. 2. Dominant community vegetation characteristics observed in the (A) Sedge, (B) Fescue), and (C) Bogbean assemblages. (D) illustration of semi-systematic plot placement along transect (red line). At least one 1 m^2 plot (black square) was placed within vegetation patches dominated by one or two species (multicolored polygons). Distance between plots varied, with minimum 1 m and maximum 10 m between all plots, regardless of the dominant species identified.

Results

Three main assemblages identified by cluster analysis, characterized by the same dominant indicator species – Sedge (*Carex lyngbyei*), Fescue (*Schedonorus arundinaceus*), and Bogbean (*Menyanthes trifoliata*) – were evident across all sampling periods (Fig. 3). The Sedge and Fescue clusters formed at lower Euclidean distance levels by 2019 suggesting that these two assemblages had become more homogeneous. While the three assemblage indicator species remained constant over time, changes were evident in other species with significant indicator values (Table 1). For example, in 1979 the indicator species defining the Sedge assemblage cluster were *C. lyngbyei, Sagittaria latifolia* Wiild., and *Schoenoplectus tabernaemontani* (C.C.Gmel.) Palla. In 1999, however, the same assemblage included indicator species *C. lyngbyei,* and *Impatiens capensis* Meerb. By 2019, *C. lyngbyei* was the only indicator for this assemblage. Similarly, *S. arundinaceus* remained a common indicator species within the Fescue assemblage, but the assemblage lost four out of seven total indicator species between 1979–2019. *Menyanthes trifoliata* consistently characterized the Bogbean assemblage, however non-native *Mentha aquatica* was common to the 1999 and 2019 datasets. For the Fescue and Bogbean assemblages, the importance of the assemblages' namesake species shifted from the highest to second highest indicator species in at least one year (Table 1); however, we elected to retain these species names as defining the assemblage as they are common to all years of observation. While the identities of the remaining indicator species changed, there was no strong trend of changes in clade, or potential difference for changes in ecological function based on a qualitative review of changing species identity.

Across the entire Ladner Marsh plant community, two to three species were lost from each sampling year following the 1979 survey (Table S6). Within every assemblage α-diversity (mean number of species per plot) decreased every observation year, while β-diversity (ratio of total species in the assemblage to α-diversity) increased each year for all assemblages (Table 2). For example, the Sedge community suffered the least loss of species and α-diversity across sampling years, although β-diversity increased as in other assemblages, indicating increasing variability in which species may be encountered within a given assemblage. The Fescue assemblage had the greatest loss of α-diversity (> 50%) between 1979 and 2019. Approximately 1/3 fewer plots clustered as Fescue in 2019 than in 1979; however, bootstrapping of 18 random plots from every sampling year showed the same trend, indicating that loss of species was not related to loss of plots (Table S3). Total magnitude of species turnover between 1999 and 2019 was ~50% in each assemblage, largely driven by greater species disappearance (loss) between 1999 and 2019 (Table S4).

Evaluation of spatial changes in assemblage locations across the marsh suggested that some shifts were related to inexact placement of transects in the 1999 and 2019 surveys (Fig. S2). For example, the relatively consistent percentage of plots within each assemblage for transects W and X implied both accuracy in transect relocation as well as plant assemblage stability. In contrast, more variable patterns in percentages, particularly for transects T, U and V, may be indicative of spatial differences in transect relocation and/or greater turnover in plot clustering among assemblages.

The greatest loss of native species richness occurred in the Fescue assemblage, while gains in non-native richness were found in all assemblages (Fig. S3). The Fescue assemblage had a net loss of 17 native species between 1979 and 2019 (Table S5). Among the species lost from the Fescue assemblage, 12 were lost from all three assemblages (six forbs, six graminoids), or were never found in any other assemblage. Species gained include two woody species, and one each of forb, graminoid, and fern ally (*Equisetum arvense* L.). There was a net loss of one non-native species in the Fescue assemblage, however non-native, invasive *Phalaris arundinacea* (reed canary grass) accounts for the greatest 2019 mean cover in the entire assemblage (25–50% mean cover, Table S5). In the Bogbean assemblage, the net gain of two non-native species included *P. arundinacea* and *Iris pseudacorus* L. (yellow flag iris). Within the Sedge assemblage, there was a net loss of two native species, and net gain of two non-native species, including *P. arundinacea* and *I. pseudacorus*. As of 2019, these species accounted for $\leq$ 25% mean cover, but may be of significant management concern (Fig. 4).

Assemblage-defining indicator species showed an overall trend of decreasing cover over time (Fig. 4). Notably, in the Fescue assemblage, the cover class of non-native indicator *S. arundinaceus* fell from a mean of ~1.5 to ~0.75 from 1979–2019, while the mean cover class of non-native *P. arundinacea* tripled from 1999–2019. In the Sedge assemblage native indicator sedge species *C. lyngbyei* decreased in cover from 1979–2019 (Fig. 4), stepping down from a mean cover class value of 3 (50–75% cover) to 2 (25–50% cover) between 1979–2019. Meanwhile, non-native species *L. salicaria* and *S. arundinaceus* increased in their mean cover abundance, although both species remained in the same mean cover class ($\leq$ 25% mean cover) by 2019. Similarly, in the Bogbean assemblage, cover abundance of native species *M. trifoliata* declined from a mean cover class of 4 (> 75%) to 3 (50-75% mean cover) by 2019, while cover of non-native *Mentha aquatica* L. increased from a mean cover class of 0.4 in 1979 (Table S5) to a mean cover class of ~2 (~25-50% mean cover) by 2019 (Fig. 4, Table S5).

Table 1 Species significantly driving cluster groups (Euclidean distance) include the same dominant species in each assemblage type (Sedge by *Carex lyngbyei*, Fescue by *Schedonorus arundinaceus*, Bogbean by *Menyanthes trifoliata*). Indicator species significantly defining the assemblage reported for p < 0.05

	1979			1999			2019		
Cluster Group Name	Species	Indicator Value	p-value	Species	Indicator Value	p-value	Species	Indicator Value	p-value
"Sedge"	*Carex lyngbyei*	0.722	<0.001	*Carex lyngbyei*	0.626	<0.001	*Carex lyngbyei*	0.591	<0.001
	Sagittaria latifolia	0.523	<0.001	*Impatiens capensis*	0.320	0.015			
	Schoenoplectus tabernaemontani	0.417	< 0.01						
"Fescue"	*Schedonorus arundinaceus*	0.607	<0.001	*Poa palustris*	0.569	<0.001	*Phalaris arundinacea*	0.518	<0.001
	Salix lasiandra	0.535	<0.001	*Schedonorus arundinaceus*	0.399	< 0.01	*Schedonorus arundinaceus*	0.461	<0.001
	Equisetum palustre	0.489	<0.001	*Trifolium wormskioldii*	0.398	< 0.01	*Equisetum fluviatile*	0.320	0.013
	Lathyrus palustris	0.433	< 0.01	*Bidens cernua*	0.371	< 0.01			
	Sidalcea hendersonii	0.331	< 0.01						
	Hordeum brachyantherum	0.293	0.016						
	Deschampsia caespitosa	0.267	0.046						
"Bogbean"	*Menyanthes trifoliata*	0.729	<0.001	*Mentha aquatica*	0.811	<0.001	*Menyanthes trifoliata*	0.942	<0.001
	Myosotis scorpiodes	0.446	< 0.01	*Menyanthes trifoliata*	0.621	<0.001	*Mentha aquatica*	0.618	<0.001
	Bidens cernua	0.407	< 0.01	Grass (unidentified)	0.452	< 0.01	*Lysimachia thyrsiflora*	0.537	<0.001
	Lythrum salicaria	0.406	< 0.01	*Lythrum salicaria*	0.424	< 0.01	*Galium trifidum*	0.465	< 0.01
	Equisetum fluviatile	0.326	0.01	*Juncus articulatus*	0.417	< 0.01	*Myosotis scorpioides*	0.392	< 0.01
	Lysimachia thyrsiflora	0.321	0.01	*Equisetum fluviatile*	0.404	< 0.01	*Juncus articulatus*	0.334	0.015
				Myosotis scorpioides	0.352	< 0.01			
				Eleocharis palustris	0.303	0.022			
				Equisetum variegatum	0.277	0.045			
				Deschampsia caespitosa	0.273	0.027			

Table 2 Data compared between 1979, 1999, and 2019 surveys resulted in five fewer species observed, lower α-diversity and greater β-diversity over time. For each assemblage type, Bogbean is the only assemblage to proportionally gain plots between 1979 and 2019, while the Fescue and Sedge assemblages lost plots. Plot loss did not appear to influence diversity components, as tested by bootstrapping a minimum of 18 plots per assemblage each year (Table S3)

	Plot-level components		**Diversity components**		
Assemblage	**No. plots**	**No. species**	**α diversity**	**α diversity sd**	**β diversity**
Sedge					
1979	34	36	8.7	2.5	3.9
1999	31	35	8.3	2.0	4.2
2019	28	34	7.9	2.7	4.3
Fescue					
1979	29	45	10.8	3.9	4.2
1999	33	41	9.7	4.0	4.2
2019	18	27	5.8	2.8	4.6
Bogbean					
1979	19	30	10.8	3.6	2.8
1999	18	36	11.5	2.9	3.1
2019	28	34	10.5	1.9	3.3
Total					
1979	82	48	10.0	3.4	4.8
1999	82	45	9.6	3.3	4.7
2019	74	44	9.4	3.0	4.7

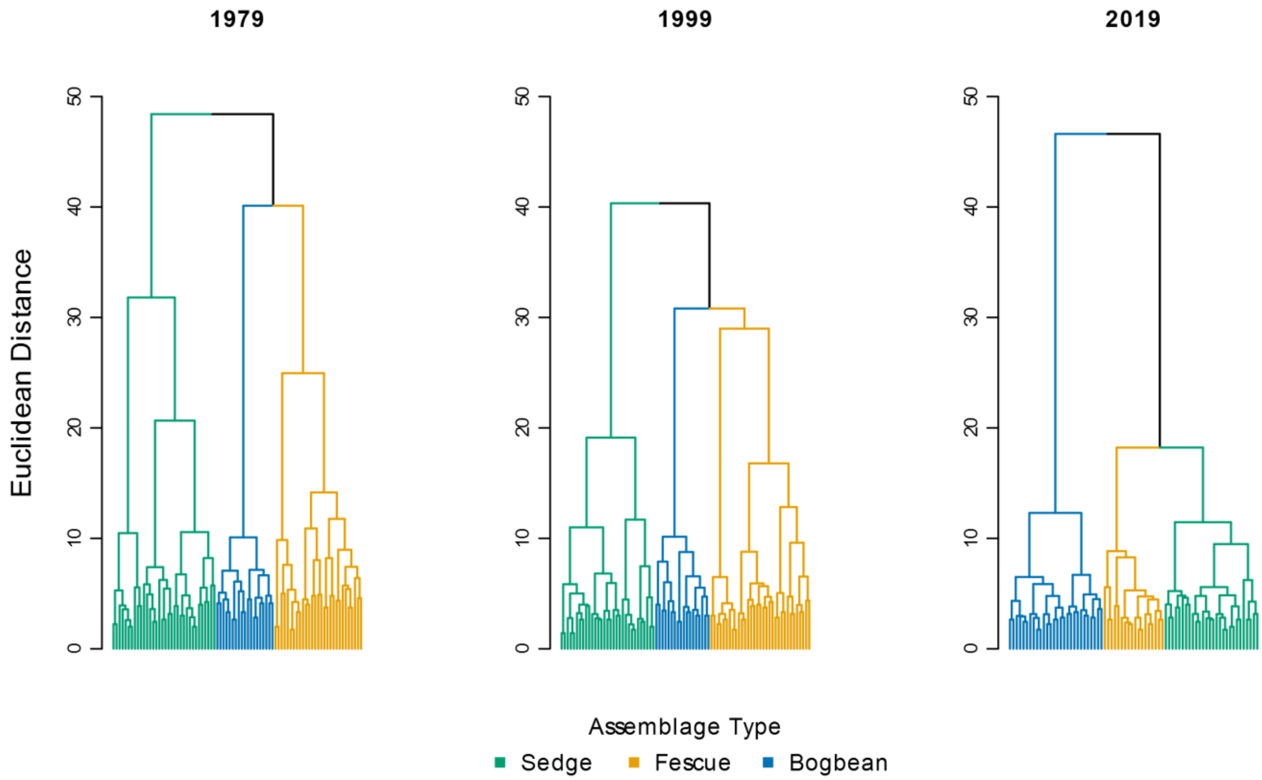

Fig. 3 Dendrograms from cluster analysis of species cover class data from each sampling period showing the three main assemblage types. Note trend towards increased homogeneity (i.e. clustering at lower distance levels) and closer similarity of Sedge and Fescue assemblages by 2019.

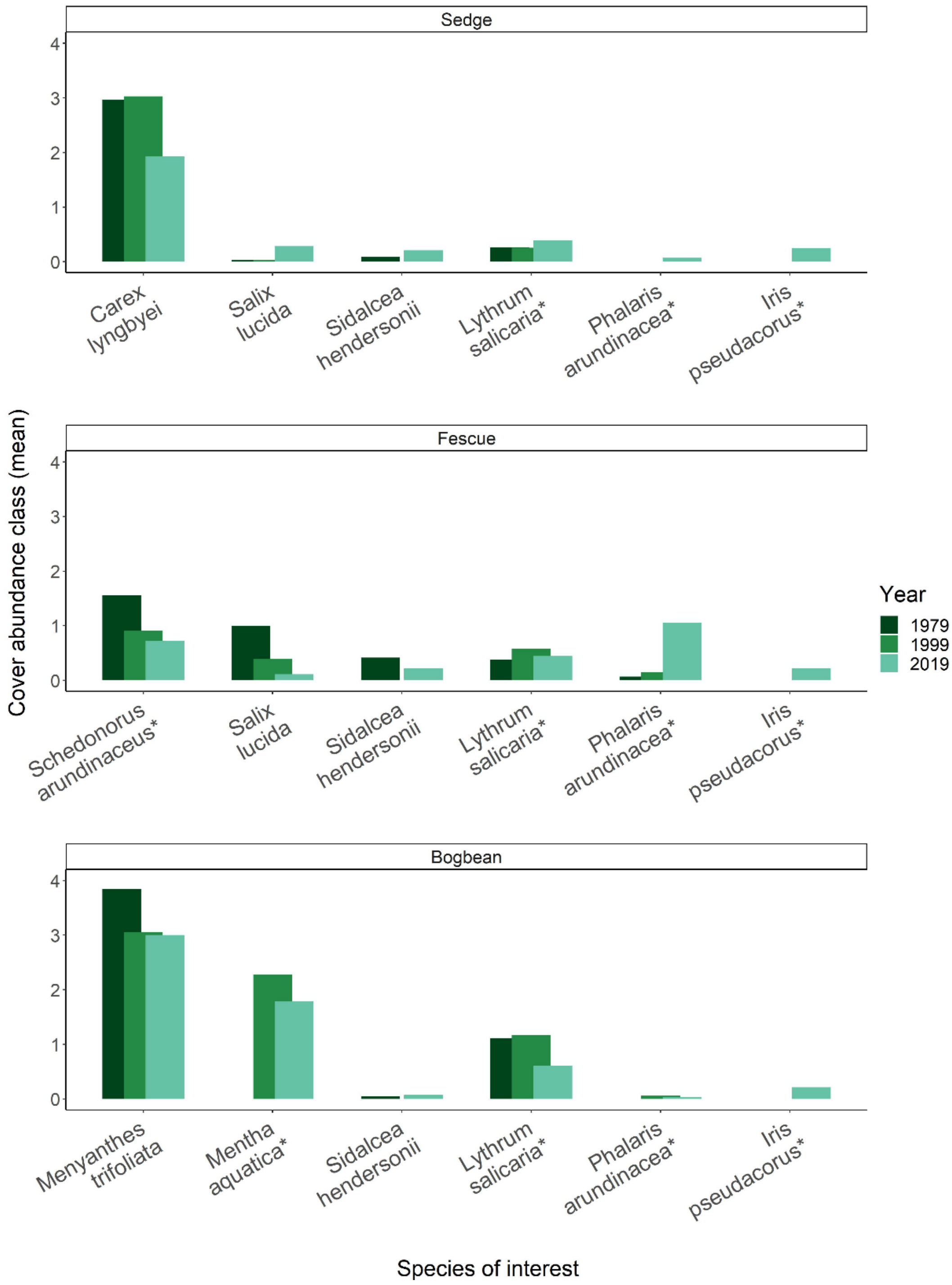

Fig. 4 Changes in mean cover abundance (cover classes) for select significant indicator species (*Carex lyngbyei, Schedonorus arundinaceus, Menyanthes trifoliata*), the most-abundant woody species (*Salix lucida*), and native/non-native species of local management interest (*Sidalcea hendersonii, Lythrum salicaria, Phalaris arundinacea, Iris pseudacorus*). Non-native species denoted by asterisk (*). Significant indicator species within each assemblage have decreased in abundance over time, while several non-native species have increased in cover abundance since 1979. Cover classes are: [1] = < 25%, [2] = 25-50%, [3] = 51-75%, [4] = >75% above-ground vegetated cover.

Discussion

Despite its status as a Wildlife Management Area and general resilience of the Fraser River tidal marsh ecosystem we found substantive changes in species composition over a 40-year time-frame, potentially indicating broader-scale processes affected by regional pressures. The three species significantly characterizing the three plant assemblages, Sedge (*C. lyngbyei*), Fescue (*S. arundinaceus*) and Bogbean (*M. trifoliata*), have remained the same over the past 40 years. We observed, however, a decline of native species richness accompanied by an increased richness and abundance of non-native species, including invasive non-native species. Of some concern is our observation of the homogenization of cover abundance within assemblages, and overall loss of indicator species for the Sedge and Fescue assemblages. Increasing abundance of non-native species within each assemblage is likely driving the greater similarity within assemblages (homogenization) and greater dissimilarity between assemblages, as shown by cluster analysis (Fig. 3). While addition of non-native species can contribute to greater biodiversity (Sagoff, 2005), the homogenization of plant communities (especially by dominance of non-native invasive species) leads to lower diversity overall (Houlahan & Findlay, 2004), which in turn may lead to lower functional redundancy and potential for reduced ecosystem stability (de Bello et al., 2021).

The changing identity of species or functional traits in an assemblage may offer clues to shifting abiotic conditions within or between assemblages (Waller et al., 2020). One functional group to note were the woody species, as their traits convey different structural habitat qualities than herbaceous species. Willow (*Salix lucida* Muhl.) was most prevalent in the Fescue assemblage in 1979, but was most abundant in the Sedge assemblage in 2019. This could suggest long-term shifts in edaphic factors, nutrient regimes, and/or the competitive encroachment of invasive reed canary grass (*Phalaris arundinacea*), making the Fescue assemblage less hospitable to willow recruitment. Alternatively, this could indicate that environmental conditions are becoming more similar between the two assemblages, as evidenced by the clustering of the Fescue and Sedge groups on the same branch in the 2019 dendrogram (Fig. 3). The indicator species analysis for the Sedge assemblage in 1979 included plants tolerant of highly saturated soils (*Sagittaria latifolia, Schoenoplectus tabernaemontani*), but in 1999 the assemblage indicators included species less tolerant of aquatic or constantly saturated soils (*Impatiens capensis*) (Table 1).

In contrast, the turnover of indicator species may simply represent variation in species compositional abundance in each sampling year, despite being a perennial-dominated community. For example, the Bogbean assemblage, was indicated largely by unique forbs in 1979 and 2019, and an even mix of unique forbs and graminoids in 1999 (Table 1). It is harder to attribute replacement of forb indicator species to potential woody riparian succession in the Bogbean assemblage as in the Sedge and Fescue assemblages. The indicator graminoid species found only in 1999 in the Bogbean assemblage (excluding an unknown grass identified only to family) are all native wetland species commonly found in brackish estuarine marshes in the Pacific Northwest of North America. Rather than indicating altered abiotic conditions, their inclusion as indicator species may simply represent population dynamics of short-lived perennials such as dispersal and recruitment. Thus, we propose two potential alternative explanations for the observed changes in floristic composition observed in the different assemblages: cumulative stressors such as altered nutrient regimes or hydrogeomorphological processes (e.g., altered sedimentation rates relative to tidal inundation) may be slowly altering abiotic conditions to favor different species within each of the assemblages identified. Alternatively, population dynamics or interspecific interactions (e.g., competition) may be operating independently of abiotic conditions, or have different outcomes depending on abiotic conditions in each assemblage. Testing how life histories (e.g., species longevity vs. recruitment) offer competitive advantage in the context of changing abiotic conditions would be a valuable long-term addition to general interactions of competition and edaphic factors. These interactions would present a valuable experimental test of competitive advantage or how edaphic conditions drive the dominance of native vs. non-native species in tidal wetlands.

Decreasing frequency of unique species within assemblages (Table 2), and increasing dissimilarity between assemblages (Fig. 3), may result from overall loss of native floristic richness. Across all assemblages in Ladner Marsh 1979–2019, we found one to two fewer native species, while β-diversity increased. This would indicate that rare (infrequently found) species are becoming more locally rare, which contributes to the loss of heterogeneous cover abundance and increased β-diversity observed at the plot scale. More concerning is the net loss of five perennial graminoid and forb species over the study period (Table S6), as this potentially represents a loss of functional redundancy. This species loss from the observed datasets may not represent species loss from the entire Ladner Marsh Wildlife Management Area. Nonetheless, the net species loss from the dataset, along with the addition of three non-native species to the datasets, poses concern for potential of species loss from the habitat over time.

Plant biodiversity loss may have consequences such as altered sediment trapping via altered vegetation structural complexity (Bouma et al., 2010) or reduce availability of important pollinator plants (Newbold et al., 2019). However, these contributions by the species lost in Ladner Marsh have not been quantified. Regardless of whether the loss is due to turnover or shifting abiotic conditions, trends of lost native plant species richness may indicate greater susceptibility to invasion (Kuiters, *et al.*, 2009), and thus a loss of resistance to non-native species encroachment over time. This can be evidenced by the decreasing ratio of native to non-native cover across Ladner Marsh 1979–2019 (Fig. S3), although few species (native or non-native) represent the majority of cover within the assemblage (Table S5). Although non-native species of significant management concern (e.g., *P. arundinacea*, *I. pseudacorus*)) were $\leq$ 25% mean plot cover in 2019, these species are notorious for spreading to the point of near-exclusion of other species (especially natives) (Apfelbaum & Sams, 1987; Sinks et al., 2021).

Mechanisms, Synthesis & Recommendations

Non-native species invasion and native species loss may lead to instability in native populations through fragmented or lost propagule dispersal networks, potentially leading to ecosystem instability through altered trophic cascades (Duffy, 2003). Disentangling explicit effects of abiotic processes of sedimentation, propagule dispersal, or propagule recruitment from other biotic interactions would be no easy task in a tidal marsh ecosystem; however, experimentally testing optimal recruitment niches of species-specific propagules (e.g., Lane, 2022) could prove valuable for understanding best practices to maintain at-risk populations or test community function.

Optimal abiotic conditions for the recruitment and spatial occupancy of native or non-native species may largely be driven by soil characteristics and related sedimentation processes. Changes such as sediment starvation, subsidence, or relative sea level rise would result in more saturated areas, which would likely drive the increased prevalence of saturated conditions favored by the Bogbean assemblage (Mendelssohn & Kuhn, 2003). Alternatively, positive feedbacks between vegetation and sedimentation could support areas of marsh accretion (Nyman et al., 2006), which may also be more likely to receive non-native propagules within the distributed sediment. While Ladner Marsh has largely escaped direct anthropogenic disturbance (e.g., industrial or agricultural development), it is subject to continuous pressures resulting from anthropogenic modifications throughout the Fraser River Estuary. Cumulative effects of altered water, sediment, and nutrient regimes impacting the lower reaches of the Fraser River can alter competitive dynamics of plant communities (Dethier & Hacker, 2005; Flores-Moreno et al., 2016), and promote the dominance of invasive species (Green & Galatowitsch, 2002; Woo & Zedler, 2002; Zedler & Kercher, 2004). In turn, this may facilitate dispersal and recruitment of non-native species and potentially limit the dispersal and recruitment of native species because propagule pools are dependent on local and regional proximity. If similar habitats within tidal estuarine ecosystems are lost to the point where distance between patches exceeds propagule dispersal distance (Shi, et al., 2020), then species colonization within the ecosystem is rare or lost (but see Stewart et al., 2022). Alternatively, if non-native species are more prevalent throughout the regional dispersal network, then there is a greater chance of non-native species introduction within a local marsh community (Briski et al., 2012).

A common (mis)assumption is that “undisturbed” protected areas such as Ladner Marsh represent ecologically appropriate reference states (e.g., Stoddard, et al., 2006, and citations therein). Our findings illustrate how, in a heavily impacted region (Finn et al., 2021), compositional states have likely shifted from recent (< 100 years) historical references, yet may still contribute value as an example of potential ecological benchmarks for restoration success (Shackelford, et al., 2021). However, the designation of Ladner Marsh as a Wildlife Management Area is likely insufficient to protect the habitat from large-scale environmental stressors in the Fraser River Estuary, such as nutrient enrichment. We suggest that the plant community changes described here should alert land managers not only to what species diversity might be targeted in conservation practice, but also to how reference sites may have changed with respect to non-native, invasive encroachment during the span of 20–40 years. We strongly advocate for the development of long-term vegetation monitoring to inform non-native invasive species management occurring in this and similar WMAs (see also Stewart, Hood, and Martin, 2023).

If we are to prioritize conservation of functional coastal wetlands that include a significant representation of native species, we must seek new ways to manage habitats such as Ladner Marsh. Active management may be required to maintain ecologically-desired species composition in the wake of environmental change, and should be informed by ongoing experimentation into the role of hydrogeomorphic drivers, dispersal networks, recruitment strategies, disturbance, and invasive species management to achieve this goal. In so doing, practitioners may enhance ecosystem processes within remnant coastal wetland habitats. This active management process also presents a timely and necessary opportunity in the Pacific Northwest of North America to engage with First Nations to revive traditional management practices in tidal wetlands, such as select mechanical disturbance (Turner, 2014). Working with traditional knowledge holders in these ecosystems may yield deeper understanding of plant community function and habitat stability, which would enhance ecosystem resilience and potentially lead to positive outcomes on regionally important salmonid and shorebird populations while contributing to reconciliation between Indigenous and colonial cultures.

Statements & Declarations

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Competing interests

The authors have no relevant financial or non-financial interests to disclose.

Author contributions

Study conception, 2019 data collection, analysis, and interpretation were undertaken by Stefanie L. Lane. Gary E. Bradfield oversaw original study design and publication (Bradfield & Porter, 1982), and advised on sampling and data analysis in this study. Madlen Denoth contributed data collected in 1999. Nancy Shackelford assisted with theoretical framework and manuscript revision. Manuscript was drafted by Stefanie L. Lane; Gary E. Bradfield, Nancy Shackelford, and Tara G. Martin participated in draft revisions on previous versions of this manuscript. All authors read and approved the final manuscript.

Data availability

Data and code for all years of observation are available on GitHub (https://github.com/stefanielane/CommunityStability.git), or via Dryad (https://doi.org/10.5061/dryad.r7sqv9sh8)

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Supplemental

Table S1 A total of 27 plots sampled in 1979 and 1999 were not sampled in 2019, mostly due to issues of accessibility. Transect names and plot ID of plots omitted follow Fig. 3 in Bradfield & Porter (1982)

Transect	1979/1999 Plot No.	Reason omitted in 2019
Q	1-7	Transect in dense riparian thicket overgrown with Himalayan blackberry
R	8	Plot on lower bench (> 1 m lower than marsh platform), vegetation no longer exists
R	17-19	Plots in 1979 & 1999 sampled across a channel. Ended transect in 2019 at channel edge.
S	33-36	Transect length in 2019 was shorter than in 1979/1999. Suspect combination of erosion and offset transect relocation altered sampling distance.
T	45	Transect length in 2019 was shorter than in 1979/1999. Suspect combination of erosion and offset transect relocation altered sampling distance.
U	51-52	Transect length in 2019 was shorter than in 1979/1999. Suspect combination of erosion and offset transect relocation altered sampling distance.
V	53	Plot 53 only plot across a channel. Increased channel width and likely erosion made crossing this channel dangerous; omitted plot in 2019.
V	54, 70-71	Transect length in 2019 was shorter than in 1979/1999. Suspect combination of erosion and offset transect relocation altered sampling distance.
W	89-92	Transect length in 2019 was shorter than in 1979/1999. Suspect combination of erosion and offset transect relocation altered sampling distance.
X	93	Transect length in 2019 was shorter than in 1979/1999. Suspect combination of erosion and offset transect relocation altered sampling distance.

Table S2 Species indicator analysis of cluster groups using Bray-Curtis distance identifies the same dominant species in each assemblage type (Sedge, Fescue, Bogbean), however Bray-Curtis distance identifies different associated indicator species than those identified by Euclidean distance (Table 1)

	1979		**1999**		**2019**	
Cluster Group Name	**Species**	**p-value**	**Species**	**p-value**	**Species**	**p-value**
"Sedge"	*Carex lyngbyei*	< 0.01	*Carex lyngbyei*	< 0.01	*Carex lyngbyei*	< 0.01
	Sagittaria latifolia	< 0.01	*Agrostis stolonifera*	< 0.01	*Mentha canadensis*	0.03
	Schoenoplectus tabernaemontani	< 0.01				
"Fescue"	*Schedonorus arundinaceus*	< 0.01	*Schedonorus arundinaceus*	< 0.01	*Phalaris arundinacea*	< 0.01
	Salix lucida	< 0.01	*Phalaris arundinacea*	0.02	*Schedonorus arundinaceus*	< 0.01
	Lathyrus palustris	< 0.01				
	Equisetum palustre	< 0.01				
	Impatiens capensis	< 0.01				
	Sidalcea hendersonii	< 0.01				
	Platanthera dilatata	0.02				
"Bogbean"	*Menyanthes trifoliata*	< 0.01	*Menyanthes trifoliata*	< 0.01	*Mentha aquatica*	< 0.01
	Myosotis scorpioides	< 0.01	*Leersia oryzoides*	< 0.01	*Menyanthes trifoliata*	< 0.01
	Juncus articulatus	< 0.01	*Mentha aquatica*	< 0.01	*Lysimachia thyrsiflora*	< 0.01
	Lythrum salicaria	< 0.01	*Bidens cernua*	< 0.01	*Salix lucida*	< 0.01
	Lysimachia thyrsiflora	< 0.01	*Lysimachia thyrsiflora*	< 0.01	*Eleocharis palustris*	< 0.01
	Trifolium wormskioldii	< 0.01	*Juncus articulatus*	< 0.01	*Juncus articulatus*	< 0.01
	Lilaeopsis occidentalis	< 0.01	*Juncus oxymeris*	0.02	*Galium trifidum*	0.01
	Mentha aquatica	0.01	*Myosotis scorpioides*	0.02	*Bidens cernua*	0.01
			Poaceae (unidentified sp.)	0.01		
			Deschampsia caespitosa	0.01		
			Sagittaria latifolia	0.05		

Table S3 Bootstrapping 18 randomly selected plots 10 times shows consistent overall trend in loss of species and alpha diversity over time, and overall increase in beta diversity between 1979 and 2019 in all assemblages and across the entire Ladner Marsh plant community. Therefore, loss of plots due to sampling re-location or how number of plots clustered into assemblages is not expected to affect loss of species or plot-based diversity metrics

	Plot-level components		Diversity components		
Assemblage	**No. quadrats**	**No. species**	**α diversity**	**α diversity sd**	**β diversity**
Sedge					
1979	18	32.3	10.67	2.34	3.03
1999	18	31.6	8.31	1.98	3.81
2019	18	30.8	8.18	2.51	3.77
Fescue					
1979	18	43	13.0	3.9	3.3
1999	18	36	9.7	3.9	3.8
2019	18	27	5.8	2.8	4.6
Bogbean					
1979	18	32	12.8	3.6	2.5
1999	18	36	11.5	2.9	3.1
2019	18	31	10.5	1.9	3.0
Total					
1979	54	48	12.2	3.5	3.9
1999	54	42	10.0	3.4	4.2
2019	54	42	8.2	3.1	5.1

Table S4 Total turnover and rates of species disappearance (loss) was always greater between 1999 and 2019 than between 1979 and 1999. However, fewer species were gained in the Bogbean assemblage 1999-2019 than 1979-1999

Assemblage	**Year**	**Total turnover**	**Species Appearance**	**Species Disappearance**
Bogbean	1979-1999	0.56	0.35	0.22
	1999-2019	0.60	0.28	0.32
Fescue	1979-1999	0.46	0.20	0.27
	1999-2019	0.64	0.18	0.46
Sedge	1979-1999	0.46	0.24	0.22
	1999-2019	0.56	0.27	0.29

Table S5 Mean cover class values for non-native and native species observed in each assemblage for each sampling period. Overall change from 1979 to 2019 indicates cover abundance decreases (-), cover abundance increases (+), and species gained or lost. For each year, blank spaces indicate no data for the species in that sampling year; blank spaces in 'Overall Change' indicate species found only in 1999.

Assemblage	Status	Species	1979	1999	2019	Overall Change (1979-2019)
Bogbean	Non-native	*Alisma plantago aquatica*	0.2	0.1		lost
		Mentha arvensis	0.5		< 0.1	-
		Myosotis scorpioides	0.7	0.2	0.2	-
		Agrostis stolonifera	3.2	1.5	1.3	-
		Lythrum salicaria	1.1	1.2	0.6	-
		Rumex conglomeratus	0.1		< 0.1	-
		Mentha aquatica	0.4	2.3	1.8	+
		Iris pseudacorus		0.3	0.2	gained
		Lycopus europaeus			< 0.1	gained
		Phalaris arundinacea		0.1	< 0.1	gained
		Festuca arundinacea		0.2		
	Native	*Alopecurus geniculatus*	0.1			lost
		Deschampsia caespitosa	0.3	0.2		lost
		Equisetum fluviatile	1.4	1.2		lost
		Leersia oryzoides	0.3	0.3		lost
		Lilaeopsis occidentalis	0.2			lost
		Oenanthe sarmentosa	0.6	0.1		lost
		Poa trivialis	0.1			lost
		Sium suave	0.6	0.2		lost
		Caltha palustris	0.9	0.2	0.1	-
		Bidens cernua	0.8	0.2	0.1	-
		Trifolium wormskioldii	0.9	0.1	0.2	-
		Schoenoplectus tabernaemontani	0.2		0.1	-
		Eleocharis palustris	0.6	0.8	0.4	-
		Symphyotrichum subspicatum	0.5	0.3	0.3	-
		Juncus oxymeris	0.1	0.1	< 0.1	-
		Platanthera dilatata	0.1	0.1	< 0.1	-
		Menyanthes trifoliata	3.8	3.1	3.0	-
		Lysimachia thyrsiflora	0.5	0.2	0.6	+
		Juncus articulatus	0.3	0.4	0.3	+
		Sidalcea hendersonii	0.1		0.1	+
		Carex lyngbyei	0.5	0.3	1.0	+
		Rumex occidentalis	0.1	0.1	0.1	+
		Potentilla anserina-pacifica	0.3	1.0	1.1	+
		Equisetum arvense			0.6	gained
		Galium trifidum			0.4	gained
		Hypericum scouleri			< 0.1	gained

Assemblage	Status	Species	1979	1999	2019	Overall Change (1979-2019)
		Impatiens capensis		0.4	0.3	gained
		Juncus acuminatus			< 0.1	gained
		Lathyrus palustris		0.1	0.5	gained
		Lysichiton americanum			0.1	gained
		Salix lasiandra		0.6	0.5	gained
		Salix scouleriana			< 0.1	gained
		Typha latifolia		0.3	0.3	gained
		Equisetum palustre		0.1		
		Equisetum variegatum		0.1		
		Galium sp.		0.1		
		Poa palustris		0.5		
		Poaceae sp.		0.3		
		Sagittaria latifolia		0.2		
Fescue	Unknown	*Festuca sp.*	< 0.1			lost
	Non-native	*Alisma plantago aquatica*	0.1	0.2		lost
		Mentha aquatica	0.3	0.1		lost
		Myosotis scorpioides	0.3	< 0.1		lost
		Mentha arvensis	0.2	0.2	0.1	-
		Festuca arundinacea	1.6	0.9	0.7	-
		Lythrum salicaria	0.4	0.6	0.4	+
		Agrostis stolonifera	0.3	0.8	0.6	+
		Phalaris arundinacea	0.1	0.2	1.1	+
		Cirsium arvense		< 0.1	0.1	gained
		Iris pseudacorus		0.2	0.2	gained
		Lycopus europaeus			0.1	gained
	Native	*Alopecurus geniculatus*	< 0.1			lost
		Bidens cernua	0.2	0.5		lost
		Deschampsia caespitosa	0.6	0.1		lost
		Dulichium arundinaceum	0.1			lost
		Eleocharis palustris	1.0	0.3		lost
		Equisetum palustre	0.8	0.1		lost
		Galium trifidum	< 0.1			lost
		Hypericum formosum	0.1			lost
		Juncus articulatus	0.5	0.1		lost
		Leersia oryzoides	0.1	0.2		lost
		Lilaeopsis occidentalis	0.2			lost
		Mimulus guttatus	< 0.1			lost
		Oenanthe sarmentosa	0.2	0.3		lost
		Platanthera dilatata	0.2	0.0		lost
		Poa palustris	0.6	1.7		lost
		Poa trivialis	0.3			lost

Assemblage	Status	Species	1979	1999	2019	Overall Change (1979-2019)
		Polygonum hydropiper	< 0.1			lost
		Sagittaria latifolia	< 0.1	0.2		lost
		Salix sp.	< 0.1			lost
		Sium suave	0.1	0.2		lost
		Symphyotrichum subspicatum	0.6	0.2		lost
		Trifolium wormskioldii	0.7	0.5		lost
		Menyanthes trifoliata	1.9	1.3	0.1	-
		Caltha palustris	0.7	0.4	0.1	-
		Salix lasiandra	1.0	0.4	0.1	-
		Carex lyngbyei	0.8	1.4	0.1	-
		Potentilla anserina-pacifica	0.5	0.6	0.2	-
		Sidalcea hendersonii	0.4	0.2	0.2	-
		Lysimachia thyrsiflora	0.1	0.3	0.1	-
		Typha latifolia	0.7	0.4	0.4	-
		Hordeum brachyantherum	0.2		0.1	-
		Equisetum fluviatile	0.6	0.4	0.4	-
		Schoenoplectus tabernaemontani	0.1	0.2	0.1	-
		Lathyrus palustris	0.6	0.2	0.6	+
		Rumex occidentalis	0.1	0.2	0.1	+
		Impatiens capensis	0.3	0.4	0.6	+
		Equisetum arvense			0.4	gained
		Juncus effusus			0.1	gained
		Lysichiton americanum			0.1	gained
		Myrica gale			0.2	gained
		Salix scouleriana			0.2	gained
		Asteraceae sp.		< 0.1		
		Carex sp.		0.1		
		Galium sp.		< 0.1		
		Juncus oxymeris		0.1		
		Salix sitchensis		< 0.1		
Sedge	Unknown	*Galium sp.*		< 0.1		
Sedge	Non-native	*Alisma plantago aquatica*	0.4	0.1		lost
		Myosotis scorpioides	< 0.1			lost
		Mentha arvensis	0.3	0.2	< 0.1	-
		Agrostis stolonifera	1.9	2.3	1.3	-
		Lythrum salicaria	0.3	0.3	0.4	+
		Festuca arundinacea	0.1	0.1	0.2	+
		Iris pseudacorus		0.1	0.3	gained
		Lycopus europaeus		< 0.1	0.1	gained
		Mentha aquatica		0.2	0.5	gained
		Phalaris arundinacea			0.1	gained

Assemblage	Status	Species	1979	1999	2019	Overall Change (1979-2019)
		Cirsium arvense		< 0.1		
	Native	*Deschampsia caespitosa*	0.2			lost
		Leersia oryzoides	0.2	0.2		lost
		Lilaeopsis occidentalis	0.1	0.1		lost
		Mimulus guttatus	0.1			lost
		Oenanthe sarmentosa	0.7	0.4		lost
		Platanthera dilatata	0.1	< 0.1		lost
		Poa palustris	1.0	0.2		lost
		Puccinellia pauciflora	< 0.1			lost
		Sium suave	0.6	0.2		lost
		Caltha palustris	1.1	0.5	< 0.1	-
		Equisetum fluviatile	0.9	0.6	< 0.1	-
		Schoenoplectus tabernaemontani	0.7	0.1	0.1	-
		Trifolium wormskioldii	0.4	0.1	0.1	-
		Sagittaria latifolia	0.4	0.1	0.1	-
		Bidens cernua	0.5	0.1	0.2	-
		Eleocharis palustris	0.8	0.4	0.4	-
		Menyanthes trifoliata	0.3	0.7	0.2	-
		Carex lyngbyei	3.0	3.0	1.9	-
		Typha latifolia	0.6	0.4	0.4	-
		Symphyotrichum subspicatum	0.3	0.1	0.3	-
		Rumex occidentalis	0.1	0.2	0.1	-
		Lysimachia thyrsiflora	0.1		0.1	+
		Sidalcea hendersonii	0.1	0.1	0.2	+
		Potentilla anserina-pacifica	0.3	0.7	0.8	+
		Rumex conglomeratus	< 0.1		0.1	+
		Lathyrus palustris	0.1	0.3	0.5	+
		Impatiens capensis	0.1	1.1	0.9	+
		Salix lasiandra	< 0.1	< 0.1	0.3	+
		Equisetum arvense			0.7	gained
		Galium palustre			< 0.1	gained
		Galium trifidum			0.1	gained
		Hypericum scouleri			0.1	gained
		Juncus articulatus			< 0.1	gained
		Juncus oxymeris			< 0.1	gained
		Scirpus microcarpus			0.1	gained
		Equisetum palustre		0.2		
		Lysichiton americanum		< 0.1		
		Salix sitchensis		0.1		

Table S6 Mean cover class values for all species recorded in each observation dataset, averaged across all plots. Across all observations, there was a net loss of five native species, and a net gain of two non-native species. Plants identified only to Family or genus are included for reference, but were not considered as a part of species net gain/loss.

Species	1979	1999	2019	Status	Change
Alisma plantago aquatica	0.22	0.12	0.00	Non-native	lost
Myosotis scorpioides	0.28	0.06	0.08	Non-native	-
Schedonorus arundinaceus	0.59	0.44	0.24	Non-native	-
Agrostis stolonifera	1.63	1.54	1.11	Non-native	-
Lythrum salicaria	0.50	0.59	0.49	Non-native	-
Rumex conglomeratus	0.02	0.00	0.05	Non-native	+
Mentha aquatica	0.20	0.60	0.88	Non-native	+
Phalaris arundinacea	0.02	0.07	0.30	Non-native	+
Cirsium arvense	0.00	0.02	0.01	Non-native	gained
Iris pseudacorus	0.00	0.18	0.23	Non-native	gained
Lycopus europaeus	0.00	0.00	0.07	Non-native	gained
Alopecurus geniculatus	0.02	0.00	0.00	Native	lost
Deschampsia caespitosa	0.37	0.09	0.00	Native	lost
Dulichium arundinaceum	0.02	0.00	0.00	Native	lost
Equisetum palustre	0.27	0.13	0.00	Native	lost
Leersia oryzoides	0.18	0.24	0.00	Native	lost
Lilaeopsis occidentalis	0.13	0.04	0.00	Native	lost
Erythranthe scouleri	0.05	0.00	0.00	Native	lost
Oenanthe sarmentosa	0.50	0.29	0.00	Native	lost
Poa palustris	0.61	0.89	0.00	Native	lost
Poa trivialis	0.13	0.00	0.00	Native	lost
Polygonum hydropiper	0.01	0.00	0.00	Native	lost
Puccinellia pauciflora	0.01	0.00	0.00	Native	lost
Sium suave	0.44	0.17	0.00	Native	lost
Caltha palustris	0.90	0.39	0.05	Native	-
Platanthera dilatata	0.12	0.04	0.01	Native	-
Equisetum fluviatile	0.90	0.62	0.12	Native	-
Trifolium wormskioldii	0.63	0.29	0.09	Native	-
Mentha canadensis	0.29	0.16	0.05	Native	-
Sagittaria latifolia	0.18	0.13	0.04	Native	-
Schoenoplectus tabernaemontani	0.35	0.10	0.08	Native	-
Bidens cernua	0.46	0.29	0.14	Native	-
Eleocharis palustris	0.82	0.44	0.30	Native	-
Hordeum brachyantherum	0.06	0.00	0.03	Native	-
Symphyotrichum subspicatum	0.44	0.22	0.22	Native	-
Juncus articulatus	0.24	0.11	0.12	Native	-
Carex lyngbyei	1.61	1.79	1.14	Native	-
Menyanthes trifoliata	1.68	1.46	1.22	Native	-

Typha latifolia	0.49	0.34	0.36		-
Sidalcea hendersonii	0.20	0.11	0.16		-
Salix lasiandra	0.37	0.30	0.32		-
Lysimachia thyrsiflora	0.20	0.18	0.27		+
Rumex occidentalis	0.09	0.15	0.12		+
Potentilla anserina-pacifica	0.35	0.76	0.76		+
Lathyrus palustris	0.23	0.20	0.50		+
Juncus oxymeris	0.01	0.06	0.03		+
Impatiens capensis	0.16	0.67	0.59		+
Galium trifidum	0.01	0.00	0.18		+
Equisetum arvense	0.00	0.00	0.59		gained
Galium palustre	0.00	0.00	0.01		gained
Juncus acuminatus	0.00	0.00	0.01		gained
Juncus effusus	0.00	0.00	0.01		gained
Lysichiton americanum	0.00	0.01	0.05		gained
Myrica gale	0.00	0.00	0.05		gained
Salix scouleriana	0.00	0.00	0.05		gained
Scirpus microcarpus	0.00	0.00	0.03		gained
Equisetum variegatum	0.00	0.02	0.00		NA
Hypericum scouleri	0.04	0.00	0.04		NA
Salix sitchensis	0.00	0.04	0.00		NA
Festuca sp.	0.01	0.00	0.00	Unknown (Not identified to species)	
Salix sp.	0.01	0.00	0.00		
Asteraceae sp.	0.00	0.01	0.00		
Carex sp.	0.00	0.02	0.00		
Galium sp.	0.00	0.04	0.00		
Poaceae sp.	0.00	0.06	0.00		

Table S7 All species recorded in 1979, 1999, and 2019, their synonymous nomenclature, and endemic status according to the Electronic Atlas of the Flora of British Columbia (E-Flora BC, https://ibis.geog.ubc.ca/biodiversity/eflora/)

Species reported 1979-2019	Synonym recorded in 1979 and/or 1999	Endemism Status
Agrostis stolonifera	*Agrostis alba*	Non-native
Alisma plantago-aquatica		Non-native
Alopecurus geniculatus		Non-native
Bidens cernua		Native
Caltha palustris		Native
Carex lyngbyei		Native
Carex sp1		NA
Carex sp2		NA
Cirsium arvense		Non-native
Composite (unidentified)		NA
Deschampsia caespitosa		Native
Dulichium arundinaceum		Native
Eleocharis palustris		Native
Erythranthe scouleri	*Mimulus guttatus*	Native
Equisetum arvense		Native
Equisetum fluviatile		Native
Equisetum variegatum		Native
Festuca sp		NA
Galium palustre		Native
Galium sp		NA
Galium trifidum	*Galium cymosum*	Native
Grass (unidentified)		NA
Hordeum brachyantherum		Native
Hypericum scouleri	*Hypericum formosum*	Native
Impatiens capensis		Non-native
Iris pseudacorus		Non-native
Juncus acuminatus		Native
Juncus articulatus		Native
Juncus effusus		Native
Juncus oxymeris		Native
Lathyrus palustris		Native
Leersia oryzoides		Native
Lilaea scilloides		Native
Lilaeopsis occidentalis		Native
Lycopus europaeus		Non-native
Lysichiton americanus		Native
Lysimachia thyrsiflora		Native
Lythrum salicaria		Non-native

Mentha aquatica	*Mentha citrata*	Non-native
Mentha canadensis		Non-native
Menyanthes trifoliata		Native
Myosotis scorpioides		Non-native
Myrica gale		Native
Oenanthe sarmentosa		Native
Phalaris arundinacea		Non-native
Platanthera dilatata		Native
Poa palustris		Native
Poa trivialis		Non-native
Polygonum hydropiper		Non-native
Potentilla pacifica		Native
Puccinellia pauciflora		Native
Rumex conglomeratus		Non-native
Rumex occidentalis		Native
Sagittaria latifolia		Native
Salix lasiandra		Native
Salix scouleriana		Native
Salix sitchensis		Native
Salix sp		NA
Schedonorus arundinaceus	*Festuca arundinacea*	Non-native
Schoenoplectus tabernaemontani	*Scirpus validus*	Native
Scirpus microcarpus		Native
Sidalcea hendersonii		Native
Sium suave		Native
Sonchus arvensis		Non-native
Symphyotrichum subspicatum	*Aster eatonii*	Native
Trifolium wormskioldii		Native
Typha latifolia		Native
Zannichellia palustris		Native

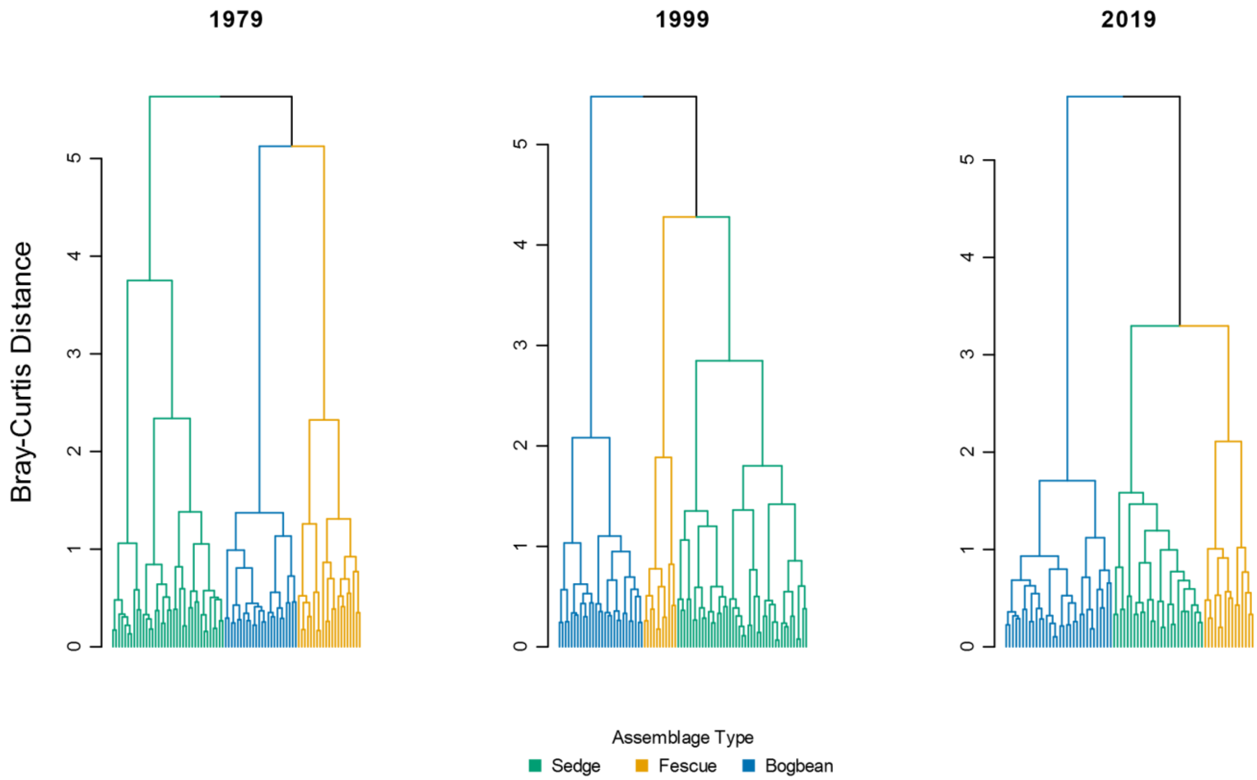

Fig. S1 Cluster analysis using Bray-Curtis distance measure shows similar trends of increasing homogeneity within assemblages as when using Euclidean distance (Fig. 3)

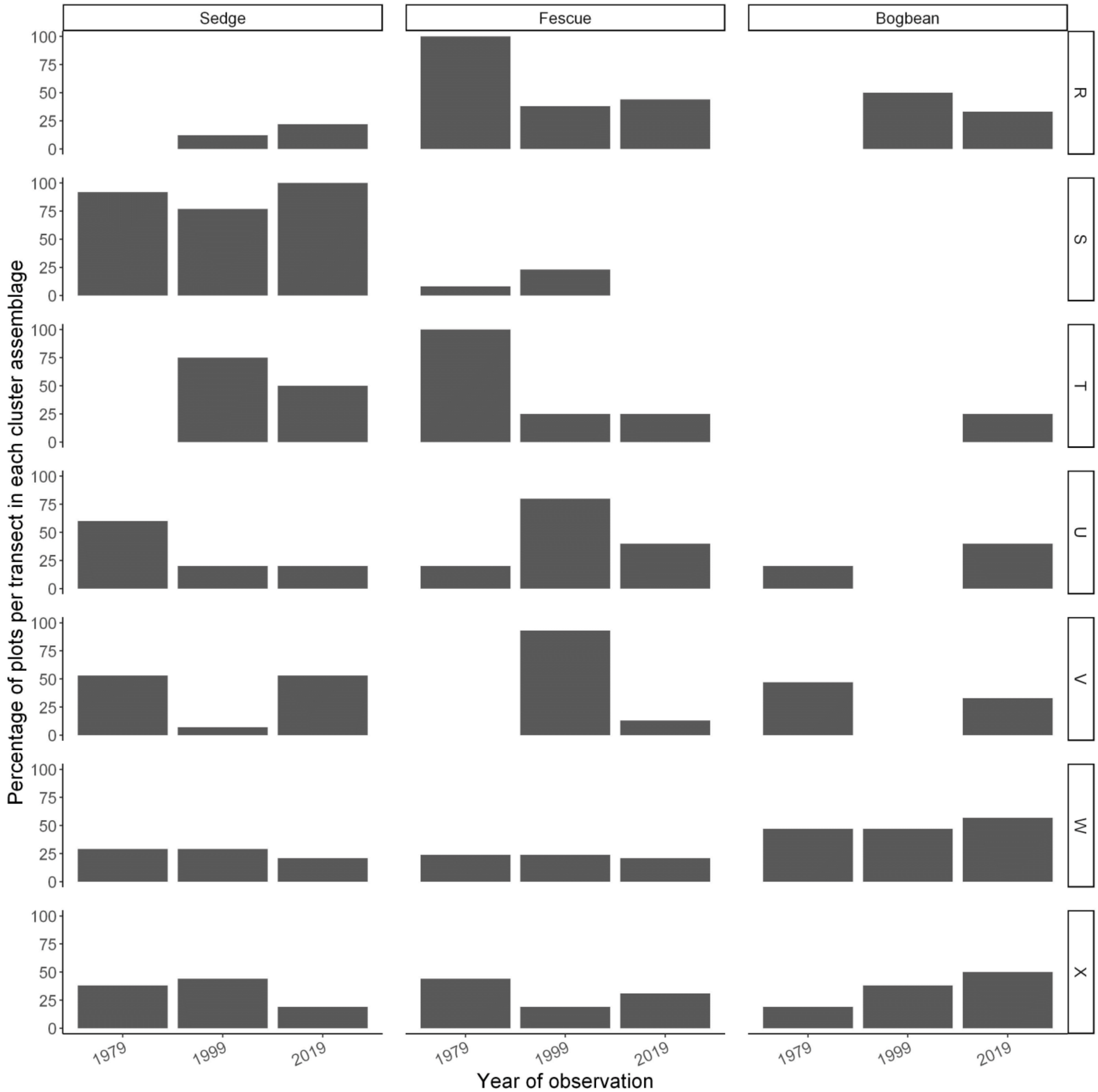

Fig. S2. Percentage of plots clustered in each assemblage calculated for each transect. Relatively even percentages of plots within each assemblage along a single transect support accuracy of transect relocation and/or plant community stability (e.g., transects W,X). Discrepancies (e.g., transects U, V) may be indicative of spatial inaccuracies in transect relocation and/or greater turnover within a given sampling year.

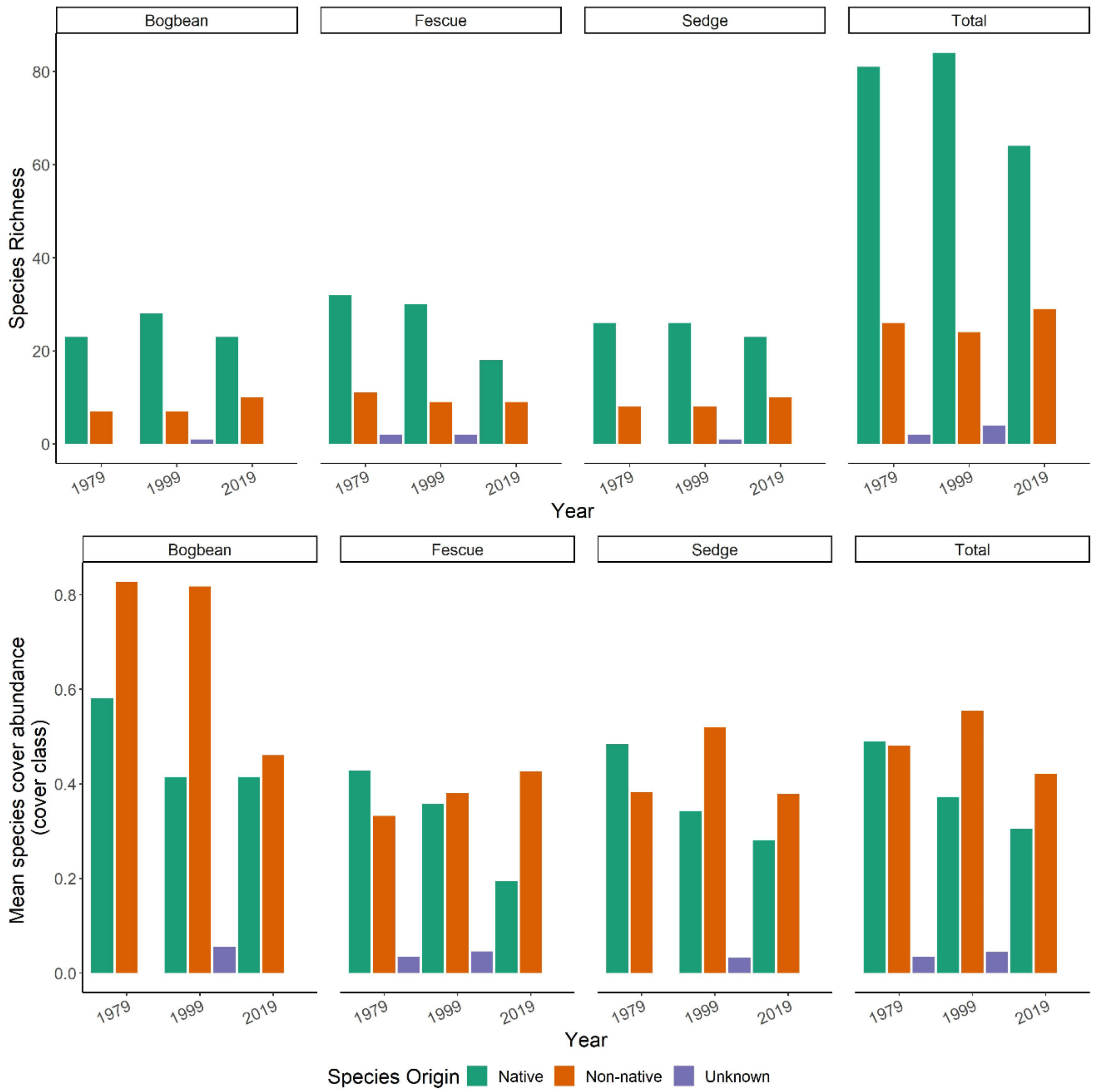

Fig. S3 Top panel: Loss of native species richness over time across all assemblages is largely driven by loss of native species from the Fescue Assemblage. However, native species richness does not change substantially in the other two assemblages. Bottom panel: Native species cover is decreasing on average across all assemblages. Non-native species cover shows a more variable pattern of change, although the ratio of native to non-native cover in Bogbean assemblage becomes more even by 2019. ‘Unknown’ species origin represents species identified only to genus, and assessment of native status cannot be made.

Reviewer response: Lane et al., Plant community compositional stability over 40 years in a Fraser River Estuary tidal freshwater marsh.

Revisions were made according to Reviewer 2 & 3 comments; we thank these reviewers for their insightful and constructive critiques. We have explained these revisions by each section of the manuscript, and indicated which reviewer we addressed for each revision.

Introduction

Reviewer 2, Line 57 (revised ms line 55): revised to include daily & monthly changes due to tide cycles, and distinguished these from processes which occur on longer timescales, such as sediment accretion or marsh subsidence.

Reviewer 2, Line 71 (revised ms line 70): changed wording from "…these habitats to resist change or recover from disturbance" to "…these habitats to adapt to disturbance."

Reviewer 3, Line 92 & Reviewer 2, Line 93: Both reviewers had concerns the hypothesis as originally phrased required substantial supporting data to link abiotic changes (e.g., altered river hydrology, sedimentation, etc.) to answer the question. We agree that these processes are important for understanding floristic responses, however it wasn't the original intent of the study nor presently possible to include these data. We revised the question (see revised ms lines 91-93) to ask "How have the tidal freshwater marsh assemblages in Ladner Marsh changed over the past 40 years? We would expect substantial changes in composition and abundance of species dominating assemblages to offer clues of processes driving change." We also advise in the Discussion on potential ways to include abiotic data in future studies to understand mechanisms driving floristic change.

Methods

To address Reviewer 2's consideration of reed canary grass as a native species, we include a brief acknowledgement of the native/non-native taxonomic debate of reed canary grass in Methods subsection Vegetation identification. We include reference to local regulatory classification, and pollen analysis to support our position treating this species as non-native in wetland communities around the Salish Sea. See revised ms lines 179-186

Reviewer 2, Fig. 1: added a scale bar & north arrow to all maps

Reviewer 2, Fig. 2D: delineation of dominant vegetation patches was confused with elevational zonation; we clarified this distinction in the figure caption.

Reviewers 2 & 3 suggested some kind of explanation of elevation and relationship to vegetation zonation along elevation gradients. In Methods subsection 'Site history & context' we clarified that the elevation gradients observed along these transects are not so great as to affect species zonation. See revised ms lines 108-119.

Reviewers 2 & 3 wanted elaboration on how/why certain transects or plots were omitted, as we described environmental changes such as channel migration and shrub encroachment as the main reasons for omitting plots. We addressed this by clarifying how Transect Q was impacted by riparian thicket encroachment, likely from immediately adjacent municipal infrastructure (revised ms lines 189-195). We also provided more detail about how inaccuracy of transect relocation may have resulted in differences in overall transect length (with speculation on some minor bank erosion also contributing to different transect length) (revised ms lines 201-210). We also provided clarification for how plot placement in 2019 would have resulted in different numbers of plots per transect, and describe how the most spatially comparable plots between all three sampling years were selected in order to make fair comparisons at the plot and transect scales (revised ms lines 201-210). This should help resolve some of the concern for not explaining broad abiotic changes: our original phrasing in the first ms submitted may have caused reviewers to infer that abiotic changes were more significant than we believe them to be. While we address these concerns (as noted elsewhere), we do not feel that abiotic changes in the marsh were the primary or secondary causes for differences in plot and transect placement over time.

Reviewer 3 specifically requested elaboration on exact methodologies to assess plant cover. We added substantial text in four new subsections to clarify the sampling design & harmonization between observations, plot-scale sampling details, and clarify differences between the datasets. (revised Methods, subsections 'Sampling design & harmonization between observations,' 'Plot-scale sampling,' 'Vegetation identification,' and 'Differences between datasets.')

In the section on analytical approach, we clarified that we elected to identify three main clusters (forgoing a common distance level break point, as suggested by Reviewer 3) to facilitate comparison of species composition & abundance between three assemblages common to all datasets (revised ms line 219-220). Because each of the three clusters identified in each dataset had consistently common indicator species (Sedge, Bogbean, Fescue), we suggest maintaining these three groupings between datasets affords the most intuitive way to discuss how composition & abundance is shifting within the marsh, especially with reference to observations made in Bradfield & Porter (1982). We also address this in the Results, as explained next.

Results

We acknowledge that analysis of the clusters at a common distance level (e.g., Euclidean distance = 35 as per Reviewer 3) would result in changing the number of groups compared, and this approach would also support our conclusion that the plant community is becoming homogenized throughout this marsh. However, indicator analysis under this approach removes Carex lyngbyei, a key marsh species, as an assemblage/indicator species only in 2019, and combines the Bogbean & Fescue groups in 1999 (but not in the 1979 or 2019 data). We feel the cumbersome explanation of these shifts in the groupings would detract from the overall interpretation of homogenization, and would not provide any further clarity on potential mechanisms for the changes. We also acknowledge that exploration of finer groupings at a lower distance level (as per Reviewer 3; e.g., Euclidean distance = 10) would allow for more discussion on finer shifts in plant composition and abundance, however, thoroughly explaining these shifts would similarly detract from the main message of homogenization without contributing benefit of identifying mechanisms.

Pursuant to this, Reviewer 3 questioned whether the 'Fescue' group should be renamed, as the namesake indicator species (Fescue, *Schedonorus arundinaceus*) shifts in its level of importance in the indicator species analysis. We propose that it is useful to have a common species to identify with each assemblage for sake of clear communication, and *Schedonorus arundinaceus* is the only common species for each observation period. Additionally, if we were alter the assemblage name for the Fescue group to reflect its shifting importance in the indicator species analysis, we would also need to do this for the Bogbean group, which further contributes to the challenge of renaming the assemblages and potentially leading to awkward communication of results. To alert readers to this convention, we include a brief statement in the Results in the explanation of indicator species analysis (revised ms line 279-282). We also amended Table 1 (indicator species results, revised ms line 328) to include the Indicator Value index as suggested by Reviewer 3, however, this creates a very wide table that requires landscape page orientation – we defer layout formatting to the editorial staff, and are happy to revise table dimensions to fit journal requirements.

We agree that an explanation of spatial relationships of the changes observed would be valuable to identify which areas of the marsh may be changing (per Reviewer 3). To this end, we included a bar chart figure of percentage of plots per transect in each cluster assemblage (Fig. S3). In the Results we explain how proportion of plots belonging to the same assemblage cluster appear quite stable along some transects (e.g., transects W and X). This allows us to speculate that some spatial trends in assemblage occurrence may be due to differences in transect placement between observation time points (e.g., transects U and V), or may be due to plant community turnover. (Revised ms lines 295-301, additional supplemental figure Fig. S2).

We agree with Reviewer 3 that the frequency with which we refer to Table S5 indicates the table is important to the Results. However, because the table is four pages long we defer to the journal's decision about whether to format it for inclusion in the Results section or as a supplemental.

Discussion

Reviewer 2 indicated hydrogeomorphological processes would need to be discussed to support the elimination of some plots from the survey due to inaccessibility and potential altered channel morphology, and Reviewer 3 wanted to see robust discussion of changes to the physical environment over time. While altered hydrogeomorphological changes are suspected drivers of change across the marsh, we feel it is beyond the scope of this study to pursue an analysis of hydrologic changes and sufficiently link these to observed plant community changes. Similarly, data on sediment transport rates in this river system would be incomplete for making a strong case directly linked to observed changes. For example, we could obtain data from sediment dredging operations, but this would not address total sediment loads. We could attempt to calculate sediment loss due to increased impervious cover on the landscape, but this would be a proxy (at best) for understanding altered sediment loading into the estuary. Instead, we have emphasized that the majority of plots eliminated from Transect Q (as reported in the original 1982 publication by Bradfield & Porter) were due to overgrowth of Himalayan blackberry, rather than channel migration. Other plots that were omitted from this analysis were clarified as likely being due to transect relocation challenges between timepoints. We acknowledge the potential for some of this relocation challenge could be due to some bank erosion, but emphasize that this would be minor (as assessed by inspection of aerial photography), and emphasize the discrepancies in transect placement as due to different observers without permanent reference markers; please also refer to revised Methods comments.

Reviewer 2, Line 339 (revised ms line 413): we indicated loss of root biomass would alter sedimentation rates; Reviewer 2 questioned whether it was only the roots or also above-ground biomass that traps sediment. We amended the language to indicate sediment trapping may be affected by altered vegetation structural complexity to indicate inclusion of any above and below-ground structures that serve to trap sediment.

Reviewer 2, Line 353: we indicated biodiversity loss can have trophic consequences, and included a reference to 'top-down trophic interactions.' Reviewer 2 pointed out this phrase was included without further explanation, so we elected to remove it as any further elaboration becomes tangential to our intended scope.

Reviewer 2, Line 361 (revised ms line 434): we focused on altered sedimentation rates as a potential mechanistic driver of change; Reviewer 2 suggested relative sea level rise as a factor, which has been added to the statement of potential mechanisms that could result in areas with greater saturation.

Reviewer 2, Line 366 (revised ms lines 439-440): ‘scouring tidal surge’ wasn’t a clear way to exemplify natural disturbance. We elected to remove reference to ‘natural disturbance,’ as the examples we could identify are confounded by anthropogenic influence over the course of our observations. For example, a ‘scouring tidal surge’ would be an extreme storm event with sufficient power to thrust large logs across the marsh, ripping out vegetation. However, current abundance of such logs within the estuary are mostly due to logging industry (rather than due to natural senescence and introduction to the estuary system). Our main point here was to indicate press stressors from anthropogenic sources are likely having an effect, despite not seeing dramatic changes commonly associated with human impacts (e.g., industrial development, agriculture, etc.); inclusion of natural disturbance in this sentence is tangential.